THE PHYLETIC CLASSIFICATION OF AMPHIPOD CRUSTACEANS: PROBLEMS IN RESOLUTION*

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ABSTRACT

The phyletic classification of amphipod crustaceans has been a major source of disagreement among principal recent workers. The disagreement results at least partly from the masking effects of convergent or homoplasious morphology not only on superfamily and subordinal recognition, but also on the determination of closest phyletic sister groups to the Amphipoda within the Malacostraca. The most recent attempts at phyletic classification of amphipods (e.g. Schram 1986, and others) are based partly on the work of the present writer, but leave important problems not entirely resolved. As a result, some recent major classifications remain alphabetical (e.g. Ruffo, 1990; Barnard & Karaman, 1991).

Based on new evidence, partly from recent behavioural work of CMN colleague K. E. Conlan, this study takes a morphological -behavioural approach to solving such problems at all levels of classification. Among malacostracan potential sister groups, the Amphipoda appears phyletically least remote from the Mysidacea, but more remote from the Hemicaridea and the Isopoda. Within the Amphipoda, two natural subordinal groups are recognized, viz, the primitive, relict Ingolfiellidea, and the more advanced, dominant Gammaridea, both with extant members in marine and freshwater habitats. Within the Gammaridea, two exclusively marine, infraordinal groups, the Hyperiidea and the Caprellidea, have possibly arisen from stegocephalid- and podocerid-like ancestors respectively.

The infraorders and superfamilies within the Gammaridea may be organized broadly and semi-phyletically into "Amphipoda Natantia" and "Amphipoda Reptantia", analogous to categories formerly employed within the malacostracan Decapoda. The former category includes reproductively free-swimming groups, with direct mating (usually lacking pre-amplexus) mostly freely in the water column. Typically here, the male is sexually specialized in the antennal sensory organs (e.g. possesses callynophore, calceoli and brush setae), eyes, and tail fan, but seldom in the gnathopods. The mature male stage is also smaller than the female and is a terminal life stage (non-moulting, often non-feeding). Components of the second category are mostly benthic or infaunal in all life stages, mating occurs on/in the bottom, with preamplexus (precopulatory grasping of the female and/or agonistic behaviour toward other males). Here also, the male is usually the larger, is usually sexually specialized in the gnathopods but not markedly in sensory organs or tail fan, and is indeterminate in growth (mates during two or more life stages). The very few anomalies within this classification are variously attributable to delayed loss of plesiomorphic structures or to convergent morphology and behaviour, in specialized forms.

INTRODUCTION

The phyletic classification of amphipods has long been frought with difficulties and much controversy among principal workers. Their views tend to be "colored" by their experiences with various taxonomic and ecological subgroupings, particularly within the Gammaridea (e.g. Bousfield (1979, 1982a, 1983); Barnard and Karaman (1980); Holsinger (1989); Stock (1985); Ruffo (1989); Lincoln (1979); Schram (1986). Contributing to this difficulty is the relatively large size of this crustacean ordinal group (more than 7000 described species in 4 suborders and more than 125 families), and the large number of external morphological characters (100+) employed variously at higher levels of classification. The current state of the problem of classification within the Amphipoda seems analogous to the tale of the three blind men who were asked to describe an elephant based on the part of the beast that each happened to be touching — trunk, leg, or tail — with three widely differing results. An overall, comprehensive, and phyletically rational picture therefore seems possible only by characterizing all body parts, of all component groups, simultaneously.

Faced with these difficulties and limitations, some authors (e.g. Ruffo et al (1990), and Barnard and Karaman (1991) have expediently adopted a simple, pragmatic, alphabetical listing of families within suborders, as is widely accepted for classifying genera within families and species within genera. However, a useful phyletic "lead" has been provided by major workers within suborder Hyperiidea (e.g. Bowman & Gruner, 1973) and Caprellidea (e.g. McCain (1970); Laubitz (1970)). Also, in order to avoid being overwhelmed by unwieldy numbers of names and volume of taxonomic detail within the much larger suborder Gammaridea, others (e.g. Lincoln (1979); Schram (1986); and the writer (Bousfield, 1979, 1983) have attempted to reduce the classificatory problem to a manageable "compromise" by utilizing a phyletically defined super family concept. Within the Gammaridea, this method reduces a

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taxonomically unwieldy 90+ families to less than two dozen readily conceptualized and readily manageable super families. Also, the number of statistically significant characters of major taxonomic value is reduced to less than 50, thereby facilitating numerical taxonomic analysis.

The need for a well founded, widely acceptable phyletic classification of amphipods, especially within the Gammaridea, is of increasing concern. Owing to new taxonomic discoveries and revisions of older taxa, species diversity within this subordinal group is increasing at the rate of about 1-2% per year. Correct family and superfamily placement of taxa such as *Aetiopedes* Moore & Myers (1988) remains highly subjective and increasingly difficult

Without a confirmed phylogeny, character states cannot be "ordered" or polarized at appropriate taxonomic levels, nor can family-level units be properly defined in relation to one another. Lack of a recognized phylogeny severely handicaps students of amphipod behaviour and physiology who require stable ancestral reference points in formulating their conclusions. Today, the Amphipoda remains one of the few major animal groups in which alphabetical classifications appear more widely utilized than phyletic arrangements. Such lack of consensus constitutes an impediment to systematic work within this subdiscipline of crustacean systematics. In our view, this problem merits further close scrutiny and, hopefully, early resolution.

The phyletic position of the other broadly recognized suborders of Amphipoda, the Hyperiidea, Caprellidea, and Ingolfiellidea viz-a-viz the Gammaridea, has been unevenly examined by previous workers. In the "pre-ingolfiellid" classical arrangements of Stebbing (1888) and Sars (1895), the hyperiids were considered among the most primitive, and the caprellids among the most advanced higher categories of amphipod crustaceans. Although recent literature on hyperiids contains little "outgroup" phyletic conjecture (e.g. Bowman & Gruner, 1973), the early status quo has apparently been maintained. With respect to the caprellids, the more recent "in-depth" studies of Laubitz (1993) and Takeuchi (1993) confirm, widely acceptably, the highly probable corophioidean origins of the caprellids, whether mono- or poly- phyletically. The morphologically advanced position of caprellids is maintained including, by inference, that of their relatively recently evolved cetacean-parasitic cyamid confreres. The small relict group of highly modified infaunal and hypogean ingolfiellid amphipods is generally considered to be phyletically very old and worthy of maintenance at subordinal level (e.g. Ruffo, 1969; Stock 1977), a view that is amplified here (pp. 120). Bowman and Abele (1982), however, would include the ingolfiellids within the Gammaridea, close to family Gammaridae.

Schram (1986) has provided one of the most recent comprehensive reviews of amphipod classification. Whereas he has acknowledged the relatively primitive phyletic position of the ingolfiellids and hyperiids, and followed phyletic arrangements of superfamilies and families within the Gammaridea proposed earlier (e.g. Bousfield, 1979, 1982a, 1983), he has placed the caprellids in a primitive position, close to the ingolfiellids. He has advocated the use of rigid cladistic techniques (e.g. a Wagner 78 program) in producing a natural classification. However, in agreement with Ridley (1983), we find many basic or "obvious" assumptions about character states to be often flawed by homoplasies; resulting cladograms in which these are not recognized are thus less realistic than phenograms in which homoplasious tendencies are selected out or otherwise minimized.

In this essay, we propose to treat the classification of amphipods phyletically, but with a somewhat semi-pragmatic approach. After the fashion of D. H.Steele (1988, et seq.) who noted that amphipods were primarily swimmers and clingers, and secondarily crawlers and burrowers, we have borrowed from older decapod crustacean classification the terms "Natantia" (for the reproductively swimming and pelagic types) and "Reptantia" (for the reproductively bottom-crawling and benthic categories). This approach utilizes reproductive (mating) morphology and behaviour, in both sexes, as its principal phyletic basis. Whatever the nature of the morphology and life style of mature females and immature stages of both sexes, reproductive morphology tends to be displayed most diagnostically in the mature male stage. Of partcular significance there is the form and armature of the antennae, gnathopods, and uropod 3 and, to some extent, in the mechanical coupling organelles of peraeopods, pleopods, and uropods. The approach also facilitates the solution, or near-solution, of some longstanding problems of natural ordering of character states, and their application at proper levels of phyletic classification.

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External Morphology of the Amphipod Crustacean.

By way of review, the general external morphology of a gaammaridean amphipod has been diagrammed previously in Bousfield (1973), Barnard & Karman (1991), and in several other popular and semi-popular works (e.g. Staude, 1987). In Figs. 1A and 1B, the principal features of representative member of Amphipoda "Natantia" and "Reptantia" respectively, are outlined.

Amphipods are similar to most members of the subclass Malacostraca (large crustaceans) in having a finitely tagmatized body; head with 5 pairs of appendages; thorax with 8 pairs (first pair fused to head as maxillipeds); abdomen with 6 pairs, and terminating in a small supra-anal flap or telson. The order Amphipoda is superficially similar to most other orders within supraorder Peracarida in which the carapace is much reduced or lacking; in having eyes that are sessile or near-sessile; mouthparts that are concentrated in a buccal mass beneath the head; thoracic legs that are uniramous (or nearly so); and lecithotropic (nonplanktonic) development of eggs within a thoracic brood pouch of the female.

Amphipods differ from all other malacostracans in having ambulatory thoracic (peraeonal) legs arranged in two distinct groups: the first four pairs are directed forwards, with the dactyls (claws) backwards, and the last three pairs are directed backwards, the dactyls forwards, hence the name "amphi"+"pod" (both kinds of feet). This contrasts with the "fan- wise" or radiating position of the thoracic legs in isopod crustaceans. A second distinctive feature, unique to amphipods, is the arrangement of abdominal limbs: the first three pairs are biramous swimming legs (pleopods) and the hind three pairs are thrusting legs (uropods). This arrangement of abdominal limbs contrasts with that , which consists of five pairs of pleopods and one pair of uropods in all other eumalacostracan crustaceans. In amphipods, tail thrust drives the animal forwards, whereas in decapods the tail thrust is typically a rearwards "escape reaction".

The diagnostic features of amphipods that mate freely in the water column (Natantia) are shown in Figure 1A, and are descibed in detail elsewhere. The body is slender, often toothed or carinate above, with large powerful abdomen, large pleopods, and lanceolate, serially spinose uropods. The head is generally short and deep, with rostrum , and eyes variously pigmented or lacking (abyssal forms). The antenna are slender and elongate. Antenna 1, peduncle stout; basal segments of flagellum often fused and strongly armed with aesthetases (chemo-sensory filaments), forming a callynophore; accessory flagellum short or lacking (in hyperiids). Antenna 2, peduncular segments 3-5 slender, anterior margin (of male) lined with fine filaments (brush setae) and often calceoli; flagellum elongate (esp. in males), often with calceoli. Mouthparts basic, mandibular and maxillipedal palps usually projecting anteriorly.

Coxal plates 1-4 various, usually shallow, similar but often unlike. Gnathopods 1 & 2 usually slender, weakly subchelate, with slender carpus and propod, seldom sexually dimorphic. Peraeopods 5-7 usually slender, usually subsimilar (homopodous), but peraeopod 6 is often longest; coxae posterolobate (hind lobe larger). Telson usually large, and bilobate (fused and plate-like in hyperiids). Coxal gills large, often pleated, on peraeopods 2-7.

Diagnositic features of benthic amphipods, the Reptantia, that mate on or in the bottom substrata, are shown in figure 1B. The body tends to be short and compact, often flattened dorsventrally, seldom with dorsal teeth or carinations. The head is usually long and shallow, lacking rostrum, eyes usually small. The antenna tend to be short, with stout peduncular segments, especially in males; callynophore and brush setae never present, and calceoli rare. Mouthparts variable, mandibular and maxillipedal palps usually visible.

Coxal plates 1-4 various, from large, deep, overlapping, to small and basally separated. Gnathopods often large, strongly subchelate, strongly sexually dimorphic. Peraeopods with relative short stout segments, and anterolobate coxae (front lobe the larger). Abdomen short; pleopods medium to reduced or highly modified. Uropods short, stout, rami linear, with apical spines. Uropod 3, rami usually short, margins spinose, or highly modified, seldom sexually dimorphic. Telson lobes variously fused, plate-like. Coxal gills plate-like or sac-like, never pleated, often lacking on peraeopod 7.

These diagnoses are intended as a generalized guide to basic amphipod morophotypes. They do not apply to any particular species, nor to immature stages. Within each group are exceptional cases that resemble species of the other group. Such encounters provide one of the frustrating "joys" of attempting to classify amphipod crustaceans.

The phylogeny of the Amphipoda as a group within the Peracarida

The phyletic positioning of the Amphipoda has also been the subject of considerable controversy. The most widely held (classical) view, that amphipods are most closely related to isopods, is held by a number of modern workers including Bowman and Abele (1982), Stock (pers. commun.) and Schram 1984, 1986). Other workers including Dahl (1963), Watling (1981), and Bousfield (1988) have presented evidence that the natural sister group among the Pericarida is the Mysidacea *(sens. lat.)*. A few others (e.g. D. H. Steele, and recently Watling (pers. communic.)) have looked for an ancestry outside the Peracarida, and do not rule out the Syncarida as the closest natural outgroup among the Eumalacostraca.

A basis for a possible mysidacean common ancestry is depicted in Figure 2. A typical gammaridean amphipod is represented by the phoxocephaloidean (lower right). At first glance, it appears to have little in common, at least externally, with the various forms of Mysidacea in the upper figures. The Mysidaceans are much more plesiomorphic in possession of a distinct maxillary carapace, and fully biramous thoracic limbs, among other differences. However, the relatively primitive ingolfiellidean amphipod (lower middle

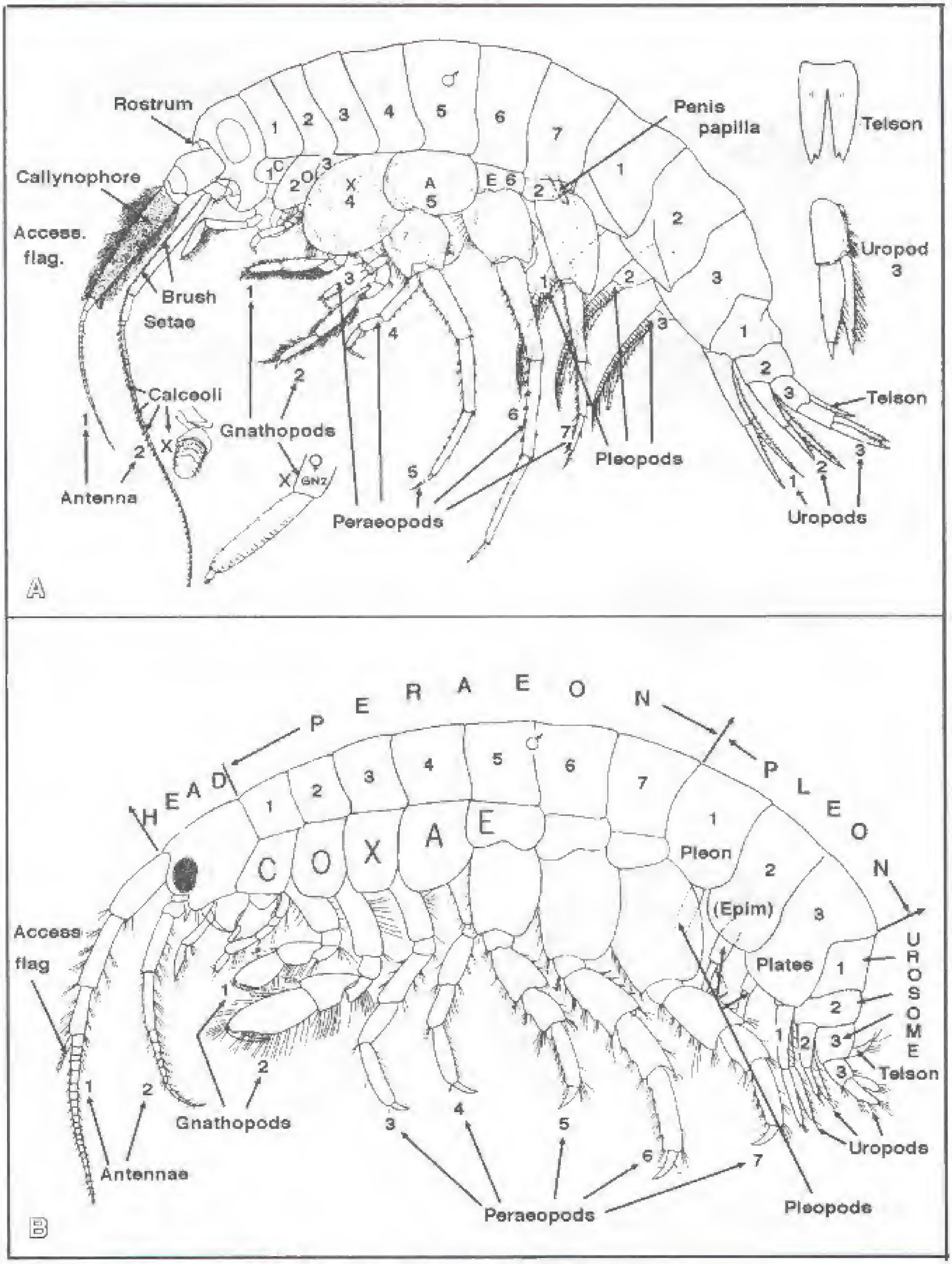


FIG. 1. Basic Morphology of the Amphipod Crustacean.
A. Natantia (Hyperiopsidae) B. Reptantia (Melitidae)

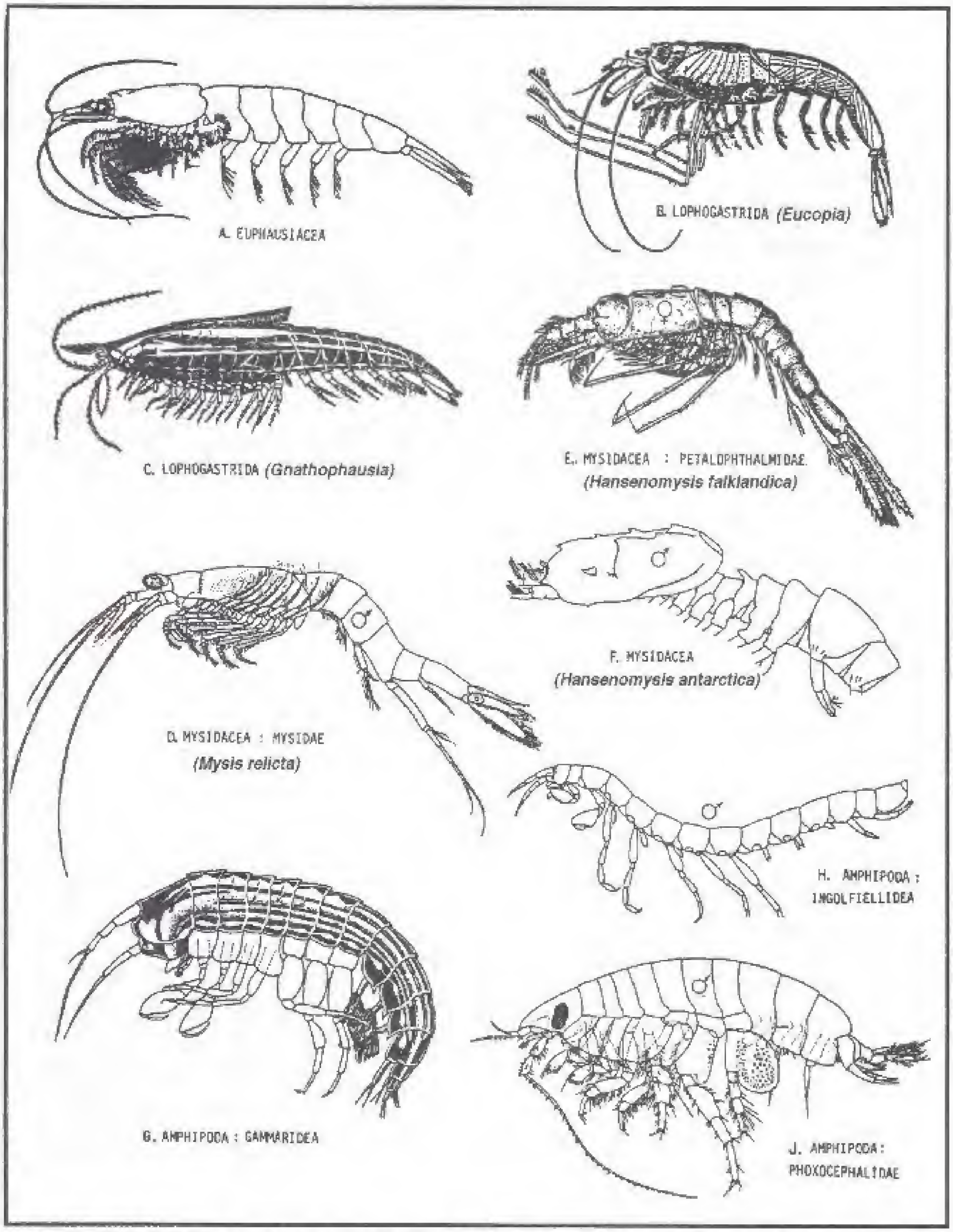


FIG. 2 EXTERNAL AND INTERNAL ANATOMICAL RELATIONSHIPS: EUPHAUSIACEA, LOPHOGASTRIDA, MYSIDA, AMPHIPODA.

(After Watling, 1981, and other sources)

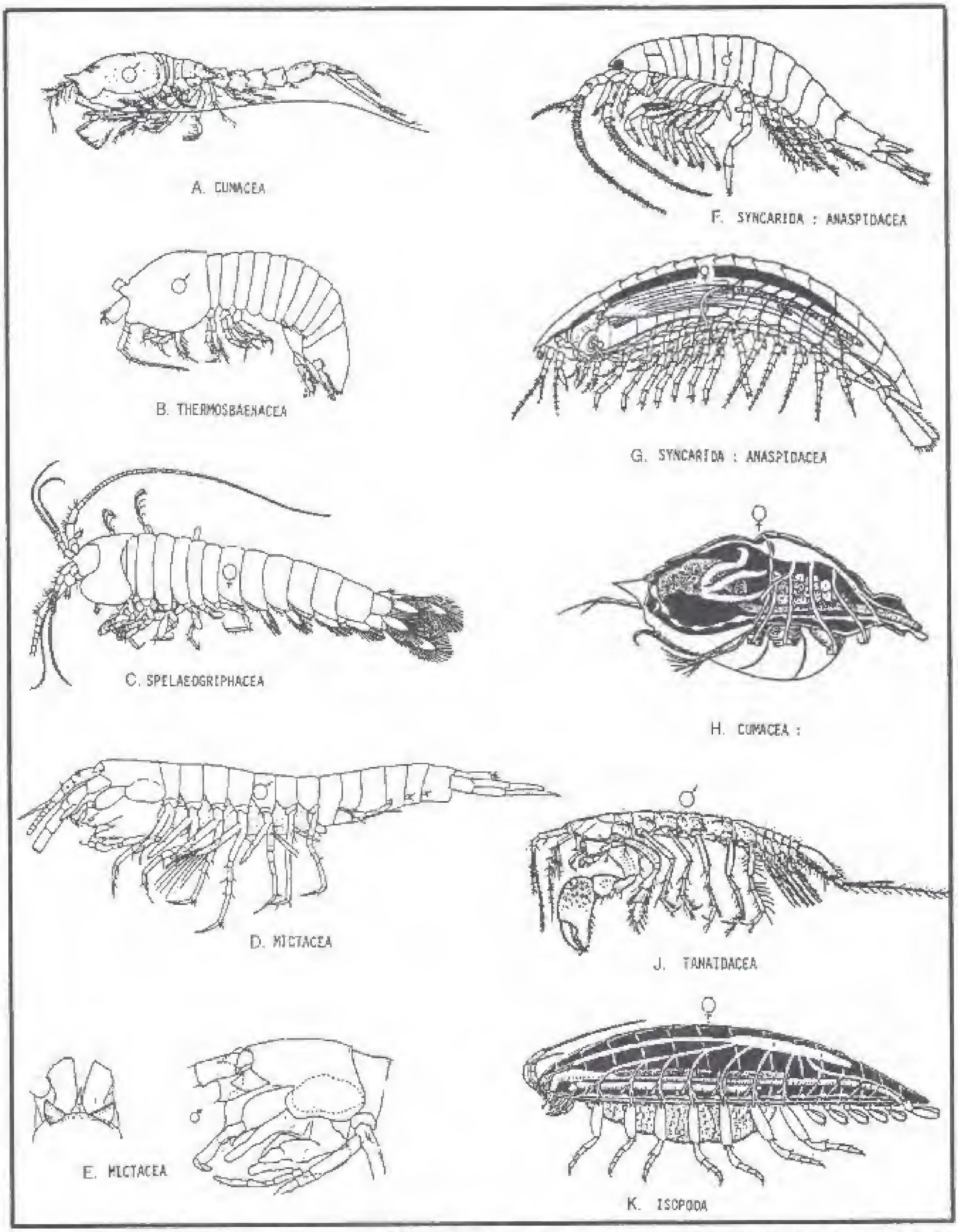


FIG 3. EXTERNAL AND INTERNAL ANATOMICAL RELATIONSHIPS OF MALACOSTRACAN SUPERORDERS SYNCARIDA, CUMACEA, BRACHYCARIDA, MICTACEA AND ISOPODA

(After Watling, 1981, Bowman & Illife, 1985, and other sources) right, and also Fig. 27) shows (1) vestigial stalked eyes, (2) partly cleft maxilliped basal segment, and (3) uropod 2 much larger and stronger than uropod 1, both with serially setose rami, as in pleopods elsewhere. All of these features are more prominently and functionally present in mysidaceans, esp. in family Petalopthtalmidae Fig. 2E. Thus, the enlarged uropod 2 of the ingolfiellidean may be homologous pleopod 5, anomalously longer than the anterior pleopods in this mysidacean family. Members of this family also demonstrate a trend to "fore and aft" subdivision of the thoracic legs, as in the Amphipoda. Also, the internal anatomy of the mysidacean (e.g. Lophogastrida, Fig. 3C), especially of the blood vascular system, with dorsal thoracic ostiate heart and thoracic respiratory vessels, is nearly identical with that of the Amphipoda (Fig. 3G; see also Watling, 1981; Schram (1986,. Mysids also possess antennal glands as well as maxillary excretory glands, a very basis and phyletically significant homology).

On the other hand, the external and internal morphology of amphipods contrasts very strongly with that of isopods and with brachycaridans (hemicarideans) (Fig. 3). In these latter taxa, the heart is weakly (or non-) ostiate, mainly (or entirely) abdominal in position, and the respiratory system is primarily abdominal, vestigially thoracic (or posteriorly cephalic). Both groups have maxillary glands but lack the primitive antennal excretory glands of amphipods. Here also, components of the buccal mass, especially the maxillae and maxillipeds, are basically differently constructed (see Schram, 1986). Other major features of these two groups, differing from the amphipods, occur in the lack of peraeopodal gill elements, and in the universal presence of flabellate (rather than annular) pleopod rami, and plate-like telson (even in juveniles). Such differences between members of these ordinal peracaridan groups are numerous and fundamental. Their similarities (in general body form and lack of carapace) appear more probably superficial and convergent. The differences probably reflect basic differencesin life-style; the amphipods being primitively swimmers, secondarily crawlers (per Steele, 1988), and the isopods and brachycaridans primitively crawlers, secondarily swimmers. All these factors, in combination, suggest a relatively remote common ancestry of amphipods and isopods, and a long period of subsequent differing evolutionary pathways. As we may note below (p. 83), the fossil record of these groups, limited as it is, tends to support such a conclusion.

With respect to the Syncarida, overall similarities (with the Amphipoda) in body form and structure of some appendages cannot be denied (see Schram, 1986). Such includes a body that is cylindrical and carapaceless, eyes that are both stalked and sessile, first thoracic segment that is fused (usually) to the head, mouthparts occurring in a loose buccal mass beneath the head, pleopod rami that are annulate, and telson that is partly cleft (in some juveniles). However, under close scrutiny, several similarities appear superficial, and comprise an anomalous mixture of primitive and advanced characteristics, many probably convergent or homoplasious. Thus, the cylindrical carapaceless body (e.g. in Anaspidacea) is only weakly tagmatized between thorax and abdomen, and metachronal swimming motion is continuous between thoracic exopods and the five pairs of abdominal pleopods. Although the pleopod rami are plesiomorphically annulate, the pleopods *per se* (except in the ancestral Palaeocaridacea) are apomorphically uniramous and usually anteriorly sexually dimorphic (Schram, 1986). The thoracic limbs (including maxillipeds) are plesiomorphically biramous, and their endopods apparently 8-(rather than 7-) segmented. Internally, although the syncarid heart is cylindrical and dorsal, it is apomorphically few- (or not) ostiate, and strongest abdominally. Also, syncarid respiration is of a more advanced type (abdominal as well as thoracic). Moreover, syncarids possess only maxillary glands and lack the primitive antennal glands that characterize amphipod excretory systems. Although syncarids and amphipods share an advanced lecithotrophic egg development, their reproductive life styles and ontogeny are very different and much less apomorphic in the Syncarida (see Schram, 1986). In combination, these character state differences appear to be at least as great as between the Amphipoda and other higher taxa within the Eumalacostraca, and suggest that a close phyletic relationship beytween the Amphipoda and the Syncarida has yet to be critically demonstrated. On the other hand, the gross character-state similarities between syncarids and amphipods may reflect modifications required by similarities in benthic, brackish- and fresh-water (possibly cold-water) life styles that are almost certainly convergent within many of the known Syncarida (including the Palaeocaridacea) and the Amphipoda. Regretably, the fossil record reveals little direct evidence bearing on such relationships (see below, p. 83).

Palaeohistorical Model

Although the fossil record of the Amphipoda is relatively limited (since Upper Eocene, Oligocene (Karaman, 1984; Bousfield & Poinar, 1993), much can be deduced indirectly from present geographical distributions and continental drift relationships, and from comparative morphology of component superfamily groups (see Bousfield, 1982b; Karaman, 1984; Schram, 1986; and Derek Briggs, pers. comunic.,). Thus, the continental freshwater distribution of component families of the primitive gammaridean superfamily Crangonyctoidea parallels that of the Astacura (Decapoda), where the fossil record is much better documented, and suggests an early Gondwanian (Mesozoic, or earlier?) ancestry. On similar grounds, the world distribution of the small group of more primitive hypogean ingolfiellid amphipods (see Stock, 1981), the gross morphology of whose epigean forebearers can only be hypothesized, would make a late Palaeozoic origin of the Amphipoda (as a whole) seem not unreasonable (see Figure 5, after Bousfield and Conlan, 1990). Such timing would be consistent with the fossil record of other peracaridan groups (e.g. Isopoda, Tanaidacea, and Cumacea) that extend back to the Lower

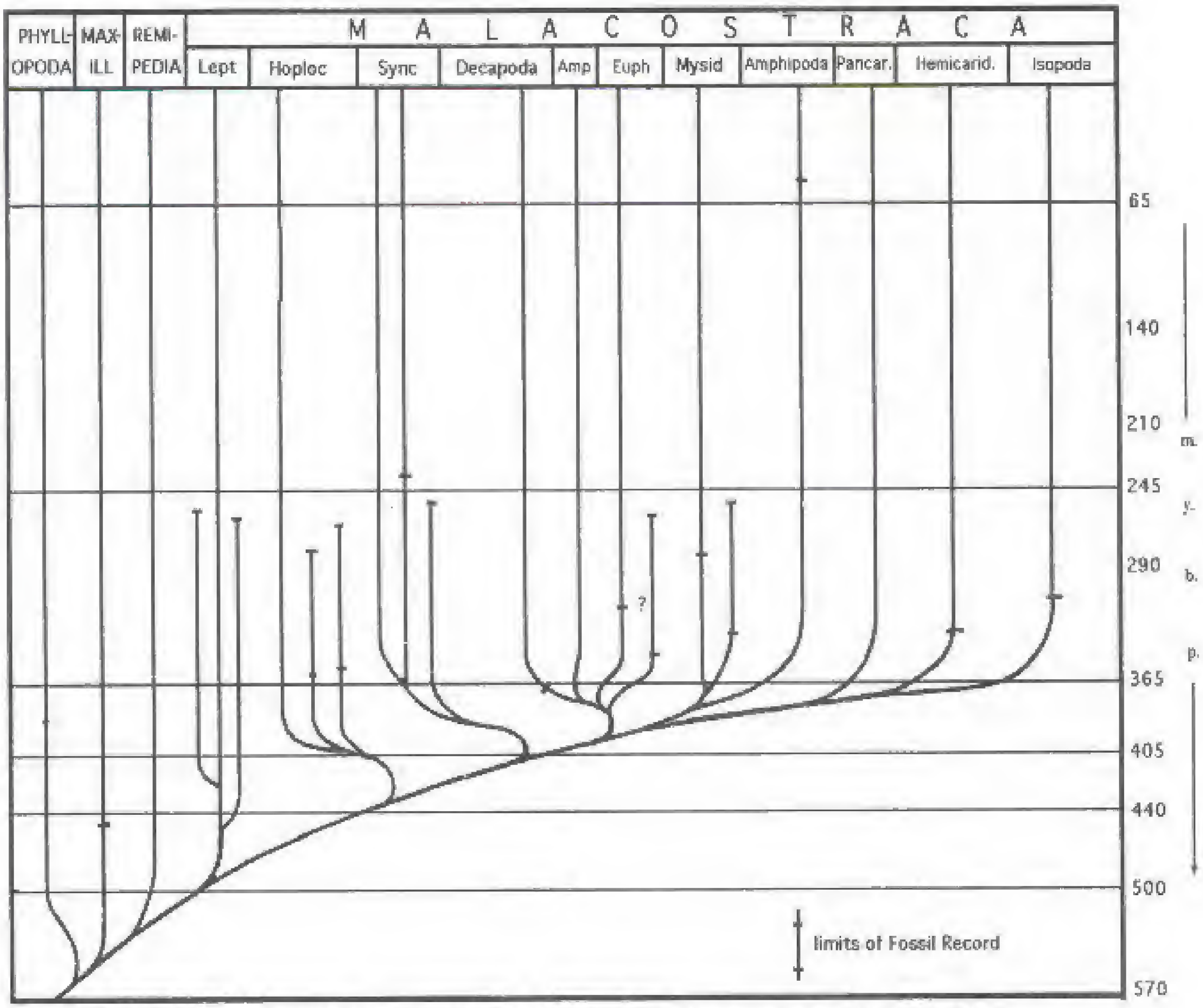


FIG. 4. PHYLOGENETIC TREE AND TIME SCALE OF THE MALACOSTRACA (after Bousfield & Conlan, 1990)

LEGEND: MAXILL - MAXILLOPODA
Lept - Leptostraca
Hoploc - Hoplocarida
Sync - Syncarida
Amp - Amphionidacea
Euph - Euphausiacea
Mysid - Mysidacea
Panc - Pancarida
Hemicarid - Hemicaridacea

Carboniferous. It is also not inconsistent with fossil records of other Eumalacostraca, for which primitive stomatopods and syncarids are recorded from various levels of the Carboniferous, and a primitive reptant decapod member (*Palaeopalaemon* , a "proto-glyphaeid") from the Upper Devonian. The earliest and most primitive crustacean groups (phyllopods, maxillipods, and even the leptostran malacostracans), were mostly small, filter-feeding and deposit-feeding marine morphotypes. Their fossil records extend back variously into the early Palaeozoic, and may indicate a possible Pre-cambrian origin for the Crustacea per se. However, the relatively abrupt appearance of major new eumal-acostracan morphotypes in the Middle to Late Palaeozoic coincides rather neatly with the contempraneous evolution and proliferation of new vascular plant groups (e.g. pteridophytes, cycads, *Cordaitales)* These relatively large, higher plant forms, along with attendant and endemic invertebrate faunas, presumably formed a basic and major new food resource for larger crustaceans in coastal terrestrial, fresh- nd brackish-water environments at this stage of palaeohistory. Ancestral amphipods, with features of a "proto-ingolfiellid" (see p. 121) may have first appeared at that time.

At any rate, the limited fossil record of the Amphipoda might indicate that most superfamily groups are of relatively recent origin and evolution, probably since mid-Mesozoic times, some 200 m.y.b.p. (Bousfield, 1982b). The highly specialized caprellidan Cymaidae cannot be much older than Eocene, when their whale hosts first exploited the food resources of Tertiary Seas. Similary, terrestrial amphipods (Talitridae) that inhabit rain forest leaf litter of Indo-Pacific and tropical rain forests, are unlikely to be older than the Cretacea\ous Period when angiosperm forests first evolved. Indeed, fossil talitrids from amber deposits of Mexico and the Dominican Republic are of Eocene Age, well within the precited time frame (Bousfield & Poinar, Jr., 1994).

A Brief History of Previous Classificatory Systems

Early classifications of the Amphipoda may be described as "arrangements" that seemd to have at least a semi-phyletic basis. Although the rationale for these arrangements seem not to have been clearly "spelled out", the first comprehensive gammaridean grouping of this type was apaparently proposed by C. S. Bate (1862) and continued among major workers by Stebbing (1888, 1906) and Sars (1895). The classifications of both hyperiids and caprellids have long been organized on a phyletic or semi-phyletic basis (e.g. in Bowman & Gruner, 1973; McCain, 1970; Vassilenko 1974; Laubitz, 1993) and sub-taxa higher than family level were often employed.

With respect to gammaridean amphipods, classificatory systems (with variants) were characterized by the early listing of groups that were strongly sexually dimorphic in sensory features (e.g. of eyes, antennae), and swimming appendages (esp. of pleopods, uropods and telson). Major taxa listed early in these treatments were presumed "primitive" and included several vegetatively fossorial families such as the lysianassids, phoxocephalids, pontoporeiids, ampeliscids and argissids. Intermediate listings included the amphilochids, stenothoids, pleustids, paramphithoids, synopiids, and families currently assigned to superfamily Eusiroidea. Advanced listings included "large-handed" types such as the Gammaridae, Liljeborgiidae, and member families of what is now the superfamily Corophioidea, but also contained some of the most strikingly spinose and ornamented groups such as the Dexaminidae, and the terrestrial Talitridae and relatives. The Caprellidea were universally considered to be the most advanced of all amphipod subordinal groups. During the first half of the 20th century, this classificatory system was followed, with little variation, by most major workers, including Chevreux & Fage (1925), Shoemaker (1930) and Gurjanova (1951).

In 1958, J. L Barnard introduced a purely pragmatic alphabetical listing of families and genera within the Gammaridea, upon which he expanded in a later descriptive and annotated compendium of world-wide families and genera (Barnard, 1969a). He informally proposed, at various times, several phyletic systems, most notably based on the "*Gammarus*" prototype, and on the "*Corophium*" (fleshy telson) ancestral type (Fig. 5). However, the "fleshy telson" thesis, expanded and detailed in subsequent papers, and in his major compendium on freshwater amphipods (Barnard & Barnard, 1983) appeared to be inconsistent with the overall morphological evidence developed by other workers. Although others soon adopted the alphabetical system (e.g. Ruffo et al (1983, 1990), his phyletic thesis received little published support elsewhere. As pointed out by Schram (1994), his co-author (in Barnard & Karaman, 1983) wrote a dissenting opinion in a separate appendix to that paper. Despite these informal phyletic proposals, the classification system of Barnard's subsequent collated works (e.g. Barnard & Barnard, 1983; Barnard & Karaman, 1991) continued to be essentially alphabetical.

Meanwhile, the need to develop a broadly acceptable basis for natural classification of related higher taxa was being more widely recognized. Bulycheva (1957) achieved a phyletic "breakthrough" by introducing the superfamily concept, Talitroidea, that combined all terrestrial talitrid and aquatic hyalid-like families. The success of this move was soon followed by J. L. Barnard's grouping of all "fleshy-telson" tube-building amphipods within newly proposed superfamily Corophioidea (1973). Similarly, the families of shallow-water gammaridean amphipods of the N. American Atlantic region were presented mainly in closely related groupings (e.g. Pontogeneiidae-Bateidae-Calliopiidae-Eusiridae, and Dexaminidae-Atylidae-Ampeliscidae) each equivalent to an informal superfamily, by Bousfield (1973).

During the mid-1970's, however, the need to group related families was matched by an equally strong need to separate out obviously unrelated major taxa that had long been submerged as informal subgroups within an "umbrella" higher category. Thus, several distinctive free-swimming or free-crawling, marine, freshwater, and hypogean groups had previously been "dumped" within an increasingly large and and unwieldy heterogeneous family concept long known as "good old Gammaridae". Similarly, several families of free-burrowing but phyletically disparate amphipods (e.g. Phoxocephalidae, Haustoriidae (Pontoporeiidae), Argissidae, the urothoids, and even the Dogielinotidae) had long been listed in close phyletic or semi-phyletic proximity (e.g by Sars (1895), Stebbing (1906), and Gurjanova (1951, 1962). The gammaroideans were soon broken up into several new superfamilies, including the Crangonyctoidea, Melphidippoidea, Melitoidea (later Hadziodea), Bogidielloidea, with various family allocations (e.g. Gammarellidae) to Eusiroidea, etc. (Bousfield, 1977). With the superfamily concept thus broadened, a phyletic arrangement of all gammaridean amphipods was then formally attempted (Bousfield, 1979a). Encouraged by the acceptance of several of these linkages by Lincoln (1979), Holsinger (1992a) and others, the superfamily and family concepts were further refined (Bousfield, 1982a, 1983). These included a phyletic sorting out of the major sand-burrowing taxa, a reclassification still in progress (e.g. Bousfield, 1989).

In support of the initial formal phyletic arrangment of superfamilies, Bousfield (1979) developed a phylogenetic tree of relationships that is examined again in this study (p.125). Trees provide a quick "visual" of basic relationships between groups of organisms, and have been widely accepted in eumalacostracan classification (e.g. Siewing, 1963). By employing numerical taxonomic methodology modified from Sneath and Sokal (1973), these relationships became more widely acceptable (Bousfield, 1983). The classification was recognized in principle in Mark Ridley's (1983) explanation of organic diversity, and incorporated in Lowry's (1986) analysis of callynophore distribution and, with some reservations, in Schram's comprehesive book on Crustacea (1986). The chart of Bousfield (1983), summarizing the range of plesio-aporphy in selected character states within 22

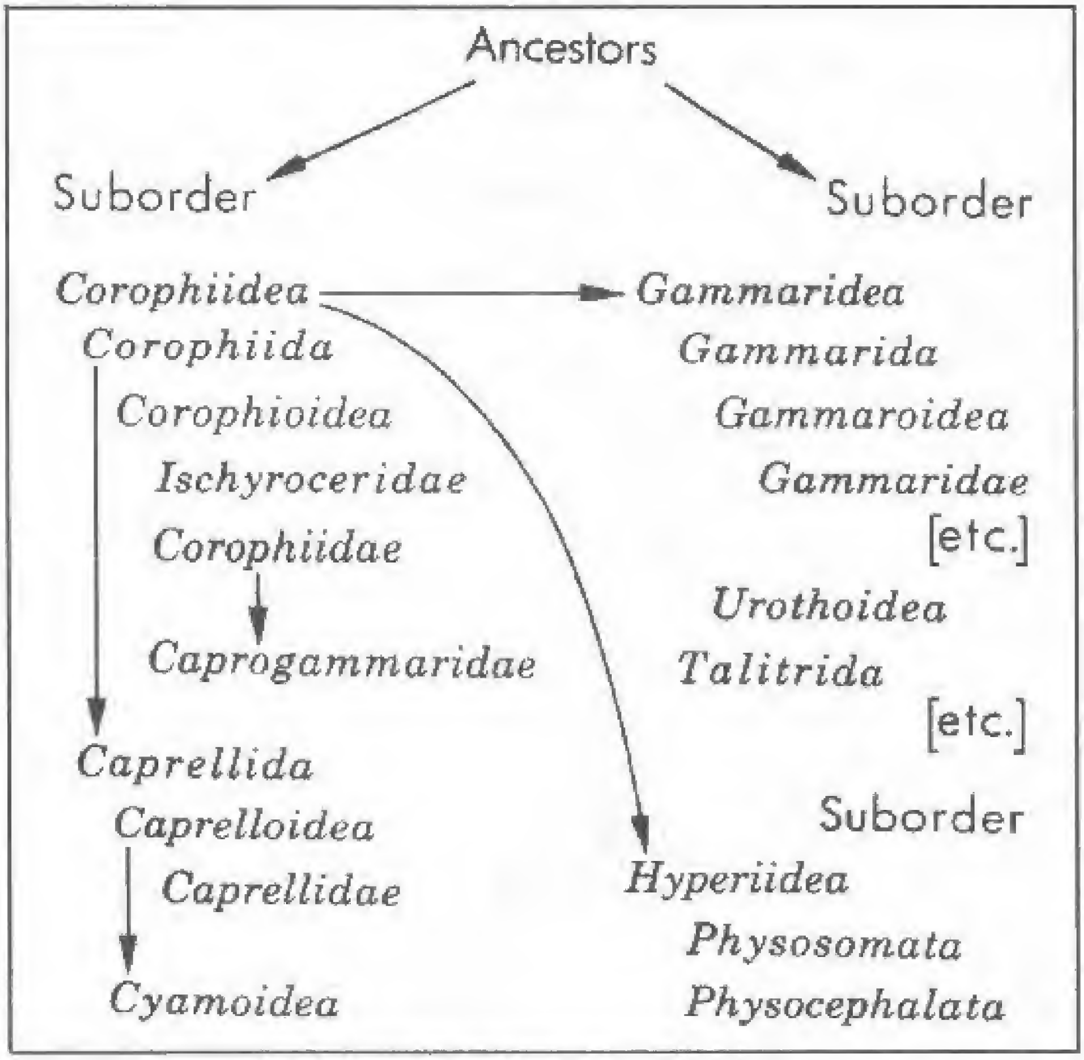
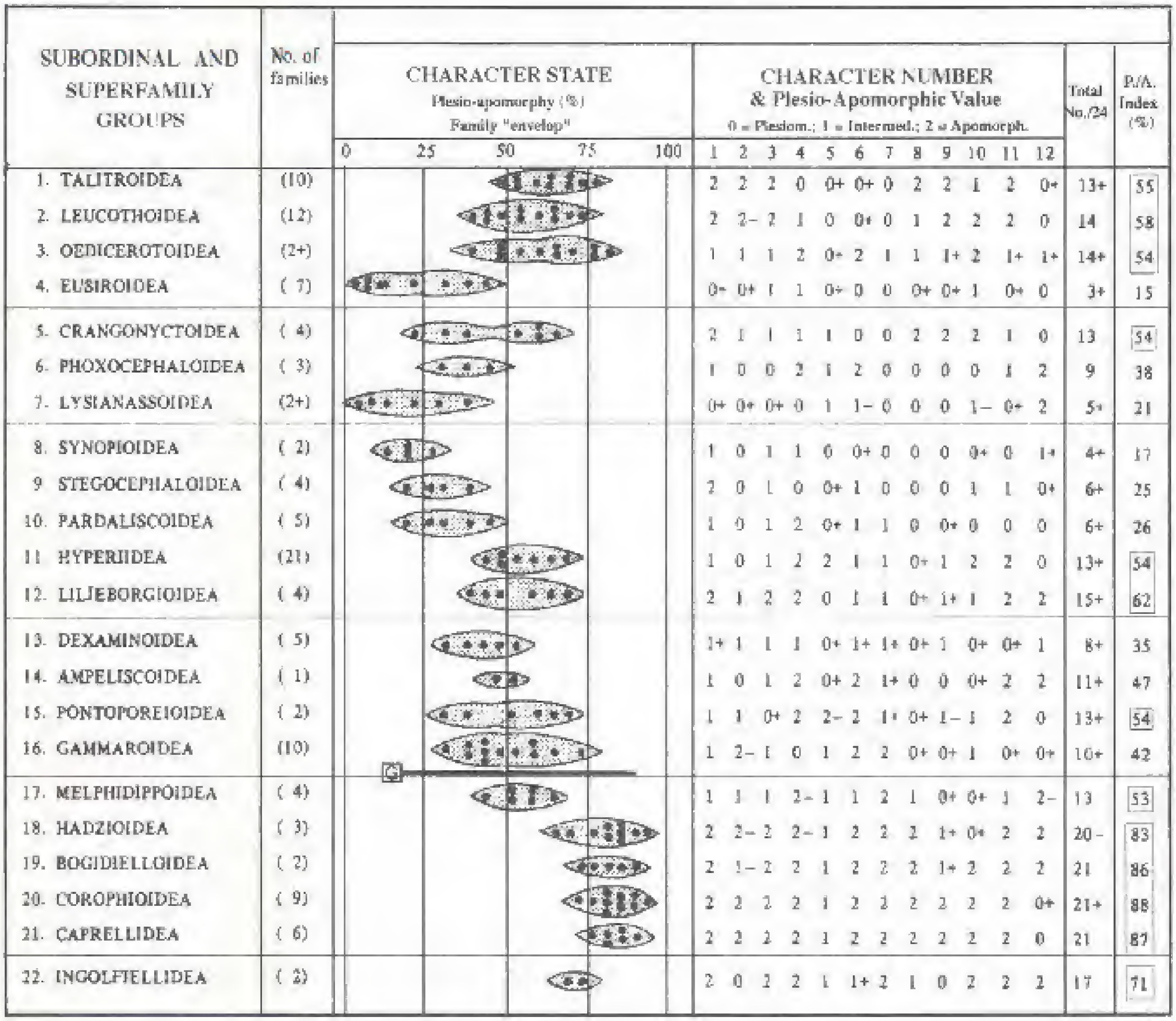


FIG. 5. PHYLETIC RELATIONSHIPS WITHIN THE AMPHIPODA PROPOSED BY J. L. BARNARD (1969).

sub-ordinal and superfamily categories within the Amphipoda is provided in Fig. 6 (p. 86). The character states are ordered, with plesio-apomorphic values of 0, 1, and 2, and the values apply to component families of the almond-shaped envelopes for each superfamily and subordinal taxon. An index of plesio-apomorphy (P./A Index) was derived by adding the values across the 12 characters for each taxon and expressing them as a percentage of 24, the highest total possible . High P/A values denote advanced, and low values primitive, taxa. In terms of present classification orientation, we may note that the envelopes for superfamilies of Natantia range mainly below, and those of the Reptantia mainly above, the 50% P/A level. A certain degree of overlap is not unexpected, where the more advanced groups of Natantia (e.g. Oedicerotidea, Hyperiidea, Pontoporeioidea) range above, and the more primitive groups of Reptantia (e.g. Crangonyctoidea, Gammaroidea) range below, the 50% level.

Recently, computer-based methodology has been more widely employed and the results more widely accepted. However, these results may not necessarily correspond to the actual route through which a group of organisms evolved. Thus, using a Wagner 78 program, Schram and Brusca had (by 1986, above) produced a cladogram of relationships among amphipod taxa that was "quite at odds with anything (then) currently in the literature". Although apparently yet unpublished, such a result would command respect. Brusca and Wilson (1991) obtained highly credible results in reclassifying the Isopoda, using a number of cladistic analysis packages that included HENNIG86 and PAUP (version 3.0). On the other hand, by means of a Wagner 78 program, Schram (1984) had employed 31 paired character states in developing 4 cladograms of relationships of major taxa within the Eumalacostraca, all of which placed the Isopoda as the phyletically closest outgroup to the Amphipoda. However, the character states found to be phyletically "synapomorphic" in these two taxa (nos. 13, 14, 21, 22, and 31 - i.e. uniramous thoracopods, pleopods lost or reduced, presence of thoracic coxal plates, eyes sessile, carapace absent) are features that are especially vulnerable to broadly eumalacostracan convergent evolution. In our view, the



SUBORDINAL AND SUPERFAMILY GROUPS	No. of families	CHARACTER NUMBER & Plesio-Apomorphic Value 0 = Plesiom.; 1 = Intermed.; 2 = Apomorph. 1	2	3	4	5	6	7	8	9	10	11	12	Total No./24	P./A. Index (%)
1. TALITROIDEA	(10)	2	2	2	0	0+	0+	0	2	2	1	2	0+	13+	55
2. LEUCOTHOIDEA	(12)	2	2–	2	1	0	0+	0	1	2	2	2	0	14	58
3. OEDICEROTOIDEA	(2+)	1	1	1	2	0+	2	1	1	1+	2	1+	1+	14+	54
4. EUSIROIDEA	(7)	0+	0+	1	1	0+	0	0	0+	0+	1	0+	0	3+	15
5. CRANGONYCTOIDEA	(4)	2	1	1	1	1	0	0	2	2	2	1	0	13	54
6. PHOXOCEPHALOIDEA	(3)	1	0	0	2	1	2	0	0	0	0	1	2	9	38
7. LYSIANASSOIDEA	(2+)	0+	0+	0+	0	1	1–	0	0	0	1–	0+	2	5+	21
8. SYNOPIOIDEA	(2)	1	0	1	1	0	0+	0	0	0	0+	0	1+	4+	17
9. STEGOCEPHALOIDEA	(4)	2	0	1	0	0+	1	0	0	0	1	1	0+	6+	25
10. PARDALISCOIDEA	(5)	1	0	1	2	0+	1	1	0	0+	0	0	0	6+	26
11. HYPERIIDEA	(21)	1	0	1	2	2	1	1	0+	1	2	2	0	13+	54
12. LILJEBORGIOIDEA	(4)	2	1	2	2	0	1	1	0+	1+	1	2	2	15+	62
13. DEXAMINOIDEA	(5)	1+	1	1	1	0+	1+	1+	0+	1	0+	0+	1	8+	35
14. AMPELISCOIDEA	(1)	1	0	1	2	0+	2	1+	0	0	0+	2	2	11+	47
15. PONTOPOREIOIDEA	(2)	1	1	0+	2	2–	2	1+	0+	1–	1	2	0	13+	54
16. GAMMAROIDEA	(10)	1	2–	1	0	1	2	2	0+	0+	1	0+	0+	10+	42
17. MELPHIDIPPOIDEA	(4)	1	1	1	2–	1	1	2	1	0+	0+	1	2–	13	53
18. HADZIOIDEA	(3)	2	2–	2	2–	1	2	2	2	1+	0+	2	2	20–	83
19. BOGIDIELLOIDEA	(2)	2	1–	2	2	1	2	2	2	1+	2	2	2	21	86
20. COROPHIOIDEA	(9)	2	2	2	2	1	2	2	2	2	2	2	0+	21+	88
21. CAPRELLIDEA	(6)	2	2	2	2	1	2	2	2	2	2	2	0	21	87
22. INGOLFIELLIDEA	(2)	2	0	2	2	1	1+	2	1	0	2	2	2	17	71

FIG. 6. RANGE OF PLESIO-APOMORPHY IN SUBORDINAL AND SUPERFAMILIES OF AMPHIPODA (AFTER BOUSFIELD, 1983)

basic differences between isopods and amphipods (e.g., in embryonic development, in mouthpart morphology, and in annulate vs. flabellate pleopods) are more significant and less subject to homoplasy; moreover, such character states of the Amphipoda find much closer parallels within the Mysidacea and Lophogastrida, as noted in the analysis of Brusca and Wilson (1991).

A recent analysis of amphipod classification, using the PAUP Version 3.0k program, has produced 5 cladograms of phylogentic relationships of amphipod families and suborders considerably at variance within anything previously published (Kim & Kim (1993). However,the validity of these results has been questioned by Schram (1994), since the anlysis of the entire amphipod taxonomic assemblage considered only 20 families (about 15% of the total) and only 16 characters (of more than 50 that could be deemed useful). A further review of that study also reveals that 10 (62%) of the selected characters concern only mouthparts, uropods, and pleopods, of essentially non-reproductive orientation, and thus of probable lesser phyletic significance.

Investigations elsewhere contribute usefully to the solution of problems of amphipod phyletic classification. Conlan (1990, 1991a) is continuing studies on the significance of sexual dimorphism of the gnathopods and of mate-guarding strategies in the phyletic relationships of corophiodean amphipods. As we find in the present study, her work applies more broadly across the superfamilies of Reptantia and across the Amphipoda generally.

Other major workers in amphipod phylogeny are investigating potential amphipod-syncarid relationships (D. H. Steele, L. Watling, personal communication). In present studies, we have yet found little evidence for such a relationship, but applaud their wide and stimulating interest in classificatory aspects of amphipod crustaceans.

A New Approach to Amphipod Phyletic Classification

As outlined previously (p. 77), the current status of phyletic classification of the Amphipoda finds no single system universally accepted or satisfactorily treating all major problems of natural relationship.

The following semi-phyletic approach to classification of amphipod crustaceans is based primarily on reproductive morphology and behaviour, as outlined recently by Conlan (1991a, b: Fig. 7, here). In summary, amphipods that search out and mate freely, usually in the water column, tend to be closely related phyletically, and may be collectively termed Amphipoda Natantia. Those that mate on or in bottom substrata, following a period of "mate-guarding" proximity between males and females, are less closely related to each other phyletically, but exhibit such similarity of life style as to be conveniently and pragmatically termed Amphipoda Reptantia. The primary features that distinguish these two principal categories are given in Table , and treated in greater detail in the following text.

Although this semi-phyletic approach covers all major groups of amphipods, at subordinal and superfamily levels, it does not pretend to solve all problemns of natural classification, at all taxonomic levels. In this essay we have attempted to tackle some of the more vexing problems, using the Natiantia-Reptantia approach in a manner that may point to ultimately correct phyletic solutions. Many problems remain unresolved and await input from yet undiscovered taxa, and broader input from more recent and more basic taxonomic tools such as ultrastructural analysis, electrophoretic serology, and eventually DNA-DNA hybridization. Especially vexing to gross morphological analysis are those taxa whose immediate characteristics are "reptant" (at family and generic level) but which prove more or less closely related to groups that are primarily "natant". We conclude that the problem of convergence is encountered in virtu-ally every facet of phyletic investigation, and allowances for this phenomenon must be made accordingly.

In the following sections we consider the phyletic significance of sexually dimorphic characters and character states, as evidenced in both the Natantia and Reptantia. In the first part of the analysis, we consider the antennal sensory organelles, reproductively significant features of the gnathopods, and phyletic trends exibited by uropod 3 and the telson. In the second part, we examine classificatory problems posed by the present status of hyperiid-gammarid and ingolfiellid-gammarid morphological relationships, and the difficulties encountered in the study of fossorial amphipods, and enigmatic hypogean taxa.

In our concluding section we present, in tabular form, a broadly revised listing of subordinal, superfamily, and family level taxa within the umbrella concept of Natantia-Reptantia. Because the concept concerning Reptantia is essentially pragmatic, and because cladistic taxonomic analysis is especially difficult to apply within the Amphipoda, our concept of higher level phyletic relationships is presented in the form of a phyletic tree, revised from previous studies.

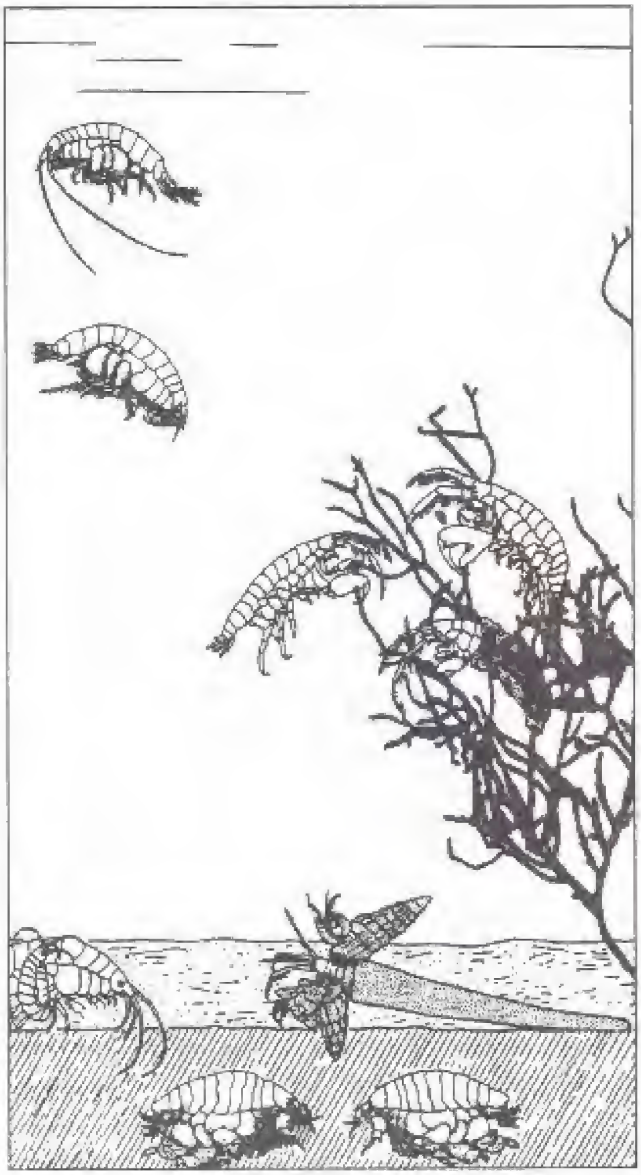


FIG. 7. Natant and Reptant Amphipoda Reproductive Setting (after Conlan, 1991).

In a more complete study, we might have included analysis of other major groups of appendages, especially the mouthparts, peraeopods, and pleopods. The significance of mouthpart morphology in the phyletic classification of amphipod crustaceans has been outlined previously for gammarideans by Bousfield (1979, 1982a, 1983, etc.) and Barnard (1969, etc.), for caprellideans by McCain (1970) and others, and for hyperiids by Bowman and Gruner (1973). In general, mouthpart morphology is a direct reflection of food preference and feeding methodology and is significant mainly at the family level of classification. Although their character states seldom mirror reproductive behaviour, certain features, especially of the mandible, are considered basic top phyletic classification. However, for development of more credible phyletic results we would advise caution in utilizing mouthpart morphology to the exclusion of reproductively significant character states.

The Natantia-Reptantia Semi-Phyletic Concept of Amphipod Classification

In a recent study of the enigmatic new gammaridean genus *Aetiopedes*, Moore and Myers (1988) opined that amphipod classification lacks a "soundly based analysis" of higher taxa or a "well founded" phylogeny. Such a comment may technically be true in a cladistical analytical sense. However, it apparently overlooks the long period of systematic stability during the first half of this century when the most widely accepted classification of amphipods was based on the semi-phyletic arrangements of Sars (1895), Stebbing (1906) and other major workers. The lack of cladistic analyses in no way prevented development of universally accepted natural classifications within other major animal groups, e.g. Mammalia, Aves, Reptilia, to name a few. In this study, the new higher classificatory concepts are based on what might be termed "first principles" that may be tested cladistically at a later stage, and are diagnosed and described as follows:

AMPHIPODA "NATANTIA"

1. Primarily strong swimmers during reproductive behaviour, even where the vegetative life style is benthic or infaunal;
2. Sexes mate freely (usually synchronously) in water column, or on/in the substratum.
3. Sexual dimorphism: in mate-seeking males, the body form, antennal size and armature, eye size, and structure of the pleopods, uropods and telson differ, usually strongly, from those of the female. Sexual dimorphism in gnathopods is weak or lacking. The male is typcially smaller than the female.
4. Male morph has a determinate moult cycle (6-8 stages); the adult stage is terminal and the male dies after mating. Females are usually semelparous.
5. The male antenna 1 is nearly always equipped with a callynophore; peduncular segments 3-5 of antenna 2, bear anterior marginal brush setae. Calceoli are frequently and variably present on one or both antennae. The flagellum of antenna 2 is frequently elongate in the male.
6. Reproductive behaviour typically does not involve pre-amplexus, except in in some Oedicerotoidea, and a few other phyletically advanced taxa.
7. Almost all taxa are exclusively marine, often with strong representation in the deep sea (Lysianassoidea, Phoxocephaloidea, Stegocephaloidea, Hyperiidea, Synopioidea, Pardaliscoidea, Dexaminioidea, Ampeliscoidea, Melphidippoidea. A few eusiroideans, melphidippoideans and allied groups (*e.g., Phreatogammarus, Sensonator*), and some oedicerotoideans inhabit fresh water, and pontoporeioideans inhabit mainly fresh or brackish waters. The vegetative life style is free-living or commensal; a few lysianassoideans and pardaliscoideans are ecto-parasitic. Some eusiroidean genera (within Pontogeneiidae and Calliopiidae) and a few melphidippoideans (*Phreatogammarus* and *Sensonator*) are hypogean in fresh water.

AMPHIPODA "REPTANTIA"

1. Primarily mate-guarders during reproductive behaviour. Free living forms tend to be carriers, an utilize gnathopods in pre-amplexus with the female until her ovulating moult. Tube builders and semi-sessile groups are mate attenders.
2. Sexes mate on or in the bottom, rarely in water column.
3. Sexual dimorphism of gnathopods is usually strong. The male is typical larger than the female but otherwise not markedly different in form. The antennae may differ in size sexually,.
4. Male morph growth stages are indeterminate(8+),with two or more sexual instars; continues to feed and mates continuously after maturity. Females are usualluy iteroparous.
5. Male antennae lack callynophore and brush setae and are seldom rarely equipped with calceoli, except in some primitive taxa. The flagellum of anntenna 2 is not elongated.
6. Mating behaviour involves involves pre-amplexus and/or mate-attending agonistic displays by males, often of lengthy duration.
7. Most groups are marine (Leucothoidea, Caprellidea) or mainly so (Hadzioidea, Lilje-borgioidea, Ingolfiellidea, Corophioidea) but with relatively limited representation in the deep sea. Nearly all have freshwater representatives. The vegetative life style is fre-living or commensal, fossorial or domicolous, and occasionally parasitic (external). The Crangonyctoidea, Gammaroidea, Bogidielloidea and Talitroidea are primarily (or nearly exclusively) freshwater and/or terrestrial. All groups except the Leucothoidea, Corophiioidea, and Caprellidea contain one or more hypogean species, and the Bogidielloidea and Ingolfiellidea are exclusively so.

The Callynophore

The possible significance of the callynophore in phyletic classification of amphipods was first introduced by Lincoln and Lowry (1984) and amplified formally by Lowry (1986). This structure consists of a bundle of generally close-set aesthetascs on the posterior, or postero-medial, margin of the fused (or conjoint) basal segments of the flagellum of antenna 1. The callynophore is distributed across a wide spectrum of amphipod taxa, including all Hyperiidea, but is characteristic of superfamily groups within the Natantia (Fig. 8). It also occurs widely across pelagic marine Malacostraca such as the Mysidacea, Lophogastrida, Euphausiacea, and Decapoda Natantia (e.g., Dendrobranchiata, Caridea) (Lowry, 1986). The structure almost certainly occurred in extinct presumably pelagic malacostracan groups such as the Pygocephalomorpha (Mysidacea) and various 'Eocaridacea' and Waterstonellidea, but present interpretation of fossil specimens does not clearly demonstrate this feature (e.g. in Schram, 1986). However, the callynophore occurs only sparsely in reproductively pelagic males of the infaunal Cumacea, and is rare (perhaps secondarily developed?) in isopods. It is apparently lacking in stomatopods, syncarids, and all other essentially benthic, reptant, or freshwater malacostracans.

With respect to function, since the callynophore consists of aesthetascs of various sizes and densities, its primary role is almost certainly chemosensory, but in some decapods may also be tactile or mechanical. In most amphipod groups the callynophore is developed only in the final adult male instar, and would seem to be of direct reproductive signifance in the detection of females within the water column. However, in some generic groups (e.g., within Lysianassoidea, Synopioidea), callynophore-like structures may also be present in mature females and subadult stages, perhaps indicating a possible secondary role in detection of food resources.

Representative forms of callynophores, within the Amphipoda, are illustrated in Fig. 8. Lowry (1986) has described a one-field arrangement of the callynophore within families Platyishnopidae, Urothoidae and Phoxocepahlidae (Phoxocephaloidea), a condition he considers primitive, and in some hyperiids (e.g. Archaeoscinidae), perhaps convergently. In all other taxa the arrangment is two-field. The callynophore is especially strongly developed in pelagic carnivores and necrophages, often where calceoli are weak or lacking, such as within the Lysianassoidea, Synopioidea, Pardaliscoidea, Stegocephaloidea, and Hyperiidea. However, with few exceptions, the callynophore is weak or lacking in reproductively pelagic but vegetatively benthic groups such as the nestling Dexaminoidea and tube-building Ampeliscoidea, and the fossorial Phoxocephaloidea and Pontoporeioidea. It is also weak or lacking in several subgroups within Natantia where the total life cycle is essentially benthic and infaunal (e.g. Haustoriidae), or commensal-parasitic (e.g. some Lysianassoidea) and/or where preamplexing reproductive behaviour has secondarily and convergently developed (e.g. in Paracalliopiidae and Exoedicerotidae within Oedicerotoidea). Curiously, the callynophore is surprisingly infrequent, or weakly developed, in the mainly marine, but mainly acalceolate family Oedicerotidae and, within superfamily Eusiroidea, is apparently restricted to the pelagic, primitive family Eusiridae.

The callynophore is almost totally lacking in the reproductively benthic Reptantia, including the Caprellidea and Ingolfiellidea, even in those that have apparently become secondarily pelagic (e.g., *Macrohectopus:* Gammaroidea). However, callynophorate-like structures have been reported from a few Amphilochidae (e.g. *Austropheonoides, Peltocoxa*) and Cressidae (*Cressa cristata*) within the primitive subgroups of Leucothoidea (Lowry, 1986).

We may reasonably conclude, therefore, that the callynophore (and its character states) offers one of the potentially most useful criteria of reproductive life style within the Amphipoda. Although its occurrence across the spectrum of amphipod superfamilies is subject to some homoplasious tendencies, such aberrancies may be correlated with non-reproductive life style and are thus predictable. In broader perspective, the presence of a callynophore is a plesiomorphic, or basic feature of malacostracan reproductive morphology, and in our view provides a primary basis for development of a phyletic classification within the Amphipoda.

Antennal Brush setae

The term "brush setae" was first applied by the author (Bousfield, 1979a) to describe the dense tufts or clusters of short brush-like setae that variously line the anterior margins of peduncular segments 3, 4, and 5, of antenna 2. A more refined term "callynosetae" might be coined from the Greek root employed by Lowry (1986) in naming the callynophore. Brush setae may occur also on the posterior (lower) margins of peduncular segments 1-3 of antenna 1 (e.g., in Dexaminoidea). To date, brush setae have been found only in the terminal male stage of pelagically reproductive amphipod superfamilies, and not yet in subadult males, females and/or immatures. They also occur in pelagic males of other peracaridan taxa such as the Cumacea and Mysidacea. Brush setae are weakly to moderately developed in calceolate amphipod taxa such as the Phoxocephaloidea, Pontoporeioidea, Eusiroidea, Oedicerotoidea, and Lysianassoidea. They are almost invariably present, and most strongly developed, in non-calceolate superfamilies of Natantia such as the Pardaliscoidea, Synopioidea, Dexaminoidea, Ampeliscoidea, and Melphidippoidea, but are less well developed or even rare within the Stegocephaloidea and Hyperiidea (Figs. 8, 30).

The function of brush setae is yet unknown and conjectural. Although they have not yet been studied in ultrastructural detail, in gross morphology they appear as modified setae, rather than thin-walled as in aesthetascs. Their role may be tactile, during the process of copulation, when the male is briefly in close contact with the female. The presence of brush setae only in males and only in plesiomorphic taxa (within the Natantia) suggests strongly that their function is of reproductive significance, and thus potentially of primary value in phyletic classification.

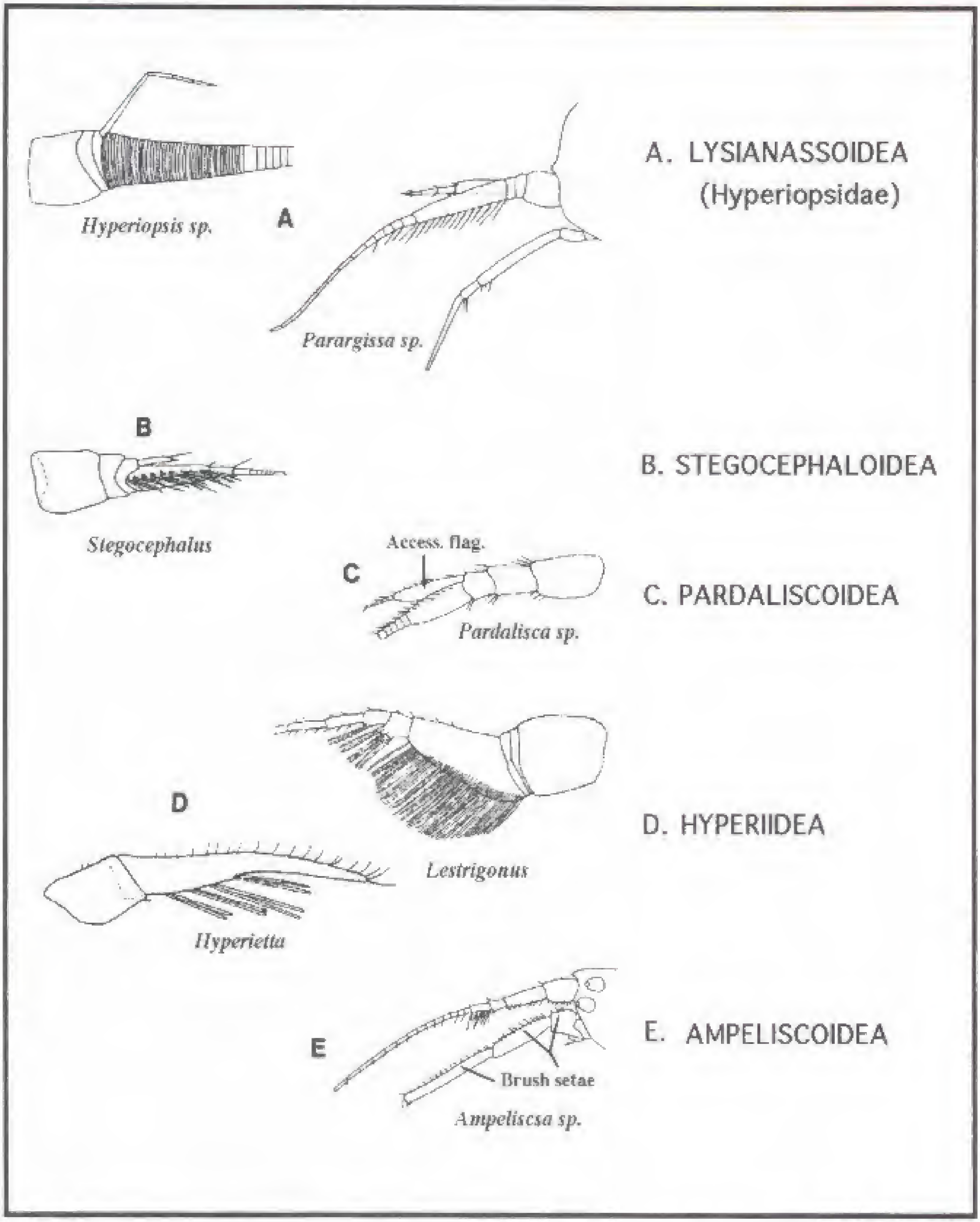


FIG. 8. TYPES OF ANTENNULAR CALLYNOPHORES
[after Barnard (1969), Bowman (1973) and other sources]

The Calceolus: Occurrence within the Amphipoda.

The possible significance of antennal calceoli in the phyletic classification of the Amphipoda has been alluded to variously by Bousfield (1979a, 1983), Lincoln and Hurley (1981), Lincoln (1984) and more recently by Godfrey, Holsinger & Carson (1988), Stapleton, Williams & Barnard (1988), Holsinger (1992), and Steele & Steele (1993).

The principal features of these antennal microstructures have been outlined by Godfrey et al (1988), with special reference to those of genera within the primitive superfamilies Crangonyctoidea and Gammaroidea of the Reptantia. The calceolus is a slipper-shaped membranous microstructure attached variously to the anteromedial segmental margins of the flagella and peduncles of both antenna 1 (antennule) and antenna 2. The combination of its structural form (in advanced forms: similar to that of a parabolic radar "dish"), and its anterior antennal location, may indicate that it functions primarily as a mechanoreceptor for detection of aquatic vibrations. However, its ennervation and connection to the brain has not yet been ascertained, nor have micro-acoustical studies yet confirmed its true function. The calceolus is not to be confused with the aesthetasc, a sublinear thin-walled microstructure of mainly chemosensory function, found only on flagellar segments of antenna 1 in nearly all species of Amphipoda. The aesthetasc also occurs widely across malacostracan ordinal subgroups, including the Decapoda. The calceolus is also readily distinguished from brush setae and other seta-like structures co-occurring on antennal peduncular and flagellar segments.

Representative types of amphipod calceoli are illustrated here (Figs. 9 &10). Calceoli-like structures are found on the proximal flagellar segments of antenna 1 (male) of a few other malacostracans, notably within the Syncarida (Anaspidacea: *Koonunga cursor*) and the Mysidacea (Mysida: *Xenacanthomysis pseudomacropsis*). Such structures are not considered calceoli by Lincoln (pers. communic.) and may be of different function, or convergent in form. However, they are included here as of possible phyletic significance within the Malacostraca and, in our view, merit further detailed comparative micro-anatomical and behavioural study.

Within the Amphipoda, the calceolus of the Crangonyctoidea (Figs. 9,10) appears to be the most simplified, and probably most plesiomorphic in form (category 9, of Lincoln and Hurley, 1981). It consists only of a basal stalk and elongate (usually narrow, occasionally distally broadened) body that bears numerous (20+) elements of similar simple structure. Holsinger (1992) has distinguished two subtypes of calceoli within the Crangonyctoidea. The calceolus of northern Crangonyctidae is slender and elongate, with an simple branched internal "tree-trunk" configuration. Some separation of basal elements in *Crangonyx richmondensis* (illustrated by Godfrey et al, 1988) are suggestive of "proto-receptacles". By contrast, the calceolus of the austral Sternophysingidae and Paramelitidae is typically broad, paddle-shaped, and its internal tree-trunk configuration has more numerous indistinct branches, a seemingly more primitive condition. In slightly more advanced types of calceoli (Fig. 10: Phoxocephaloidea), the elements are fewer (10-15 in Platyischnopidae; 4-6 in Phoxocephalidae); and the body may be short and spatulate, or barrel-shaped, as in some Phoxocephalidae.

In more advanced types of calceoli, the basal element is broadened and modified into a receptacle (weakly developed in Pontoporeioidea and Gammaroidea, strongly so in Eusiroidea), and the stalk is distally expanded into a bulla or resonator, weakly and more strongly in those same groups, respectively. In some Pontoporeioidea (Bathyporeiidae), finger-like processes protrude over the proximal elements. In the most advanced types of calceoli (viz., in some Eusiroidea: Gammarellidae, Eusiridae; Fig. 9), and in some pelagic Lysianassoidea (e.g. *Ichnopus* spp., Lowry and Stoddart, 1992), the distal elements are few and widely separated from one or more large, cup-shaped receptacles, and the bulla is prominent.

With respect to the Eusiroidea, Steele & Steele (1993) found two types of calceoli in *Gammarellus angulosus*, viz, a large "pontogeneiid" type and a smaller, but more complex "gammarellid" type. The former occurred singly only on flagellar segments of first and second antennae of mature males. The latter were found encircling the flagellar segments of larger immatures and females as well as mature males. Although Steele & Steele (loc. cit.) have urged caution in the use of calceoli in higher classification, their work may be interpreted as directly supportive of such use. Thus, the basic pontogeneiid type, in males only, would directly link the Gammarellidae to other families with similar male-only calceoli, now placed within superfamily Eusiroidea. The smaller, more specialized calceoli of all sexes and stages of *Gammarellus*, are almost certainly not reproductively significant. Instead, these may assist in the detection of pelagic prey organisms by all life stages of these raptorial predators.

The evolutionary morphological sequence within the calceoli portrayed here is believed to match more closely the phylogeny of corresponding superfamily groups, based on other character states (see below), than does the somewhat pragmatic sequence originally provided by Lincoln and Hurley (1981).

A graphical plot of the types of calceoli and their distribution by antennal site, sex, and higher taxon, can be linked by means of a branching arrangement with relationships that, in part, are remarkably similar to phyletic arrangements derived elsewhere from analysis of other character states (Figure 11). In the first two categories, this arrangement goes somewhat beyond the relationships proposed by Lincoln (1984) on the basis of the taxonomic (classificatory) distribution of calceoli. In the present chart, the positions of the major taxa in the various "boxes" are correlated primarily with the distribution (or lack) of calceoli on one or other (or both) antennae, along the horizontal axis and with the morphological type and its sexual occurrence,

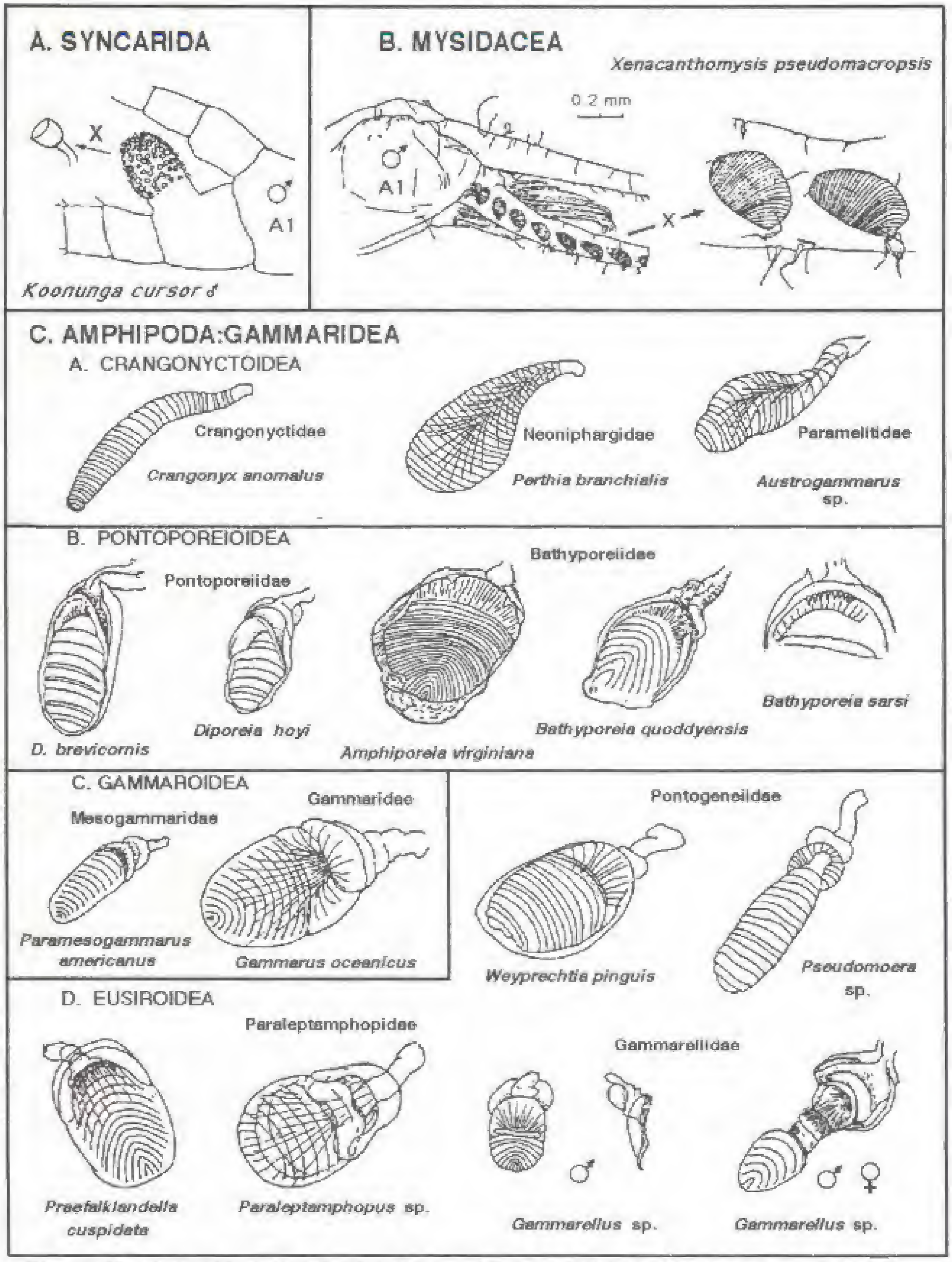


FIG. 9. TYPES OF CALCEOLI IN GAMMARIDEAN AMPHIPODA AND POSITIONALLY SIMILAR ORGANELLES IN OTHER MALACOSTRACANS [modified from Lincoln & Hurley (1981) and other sources]

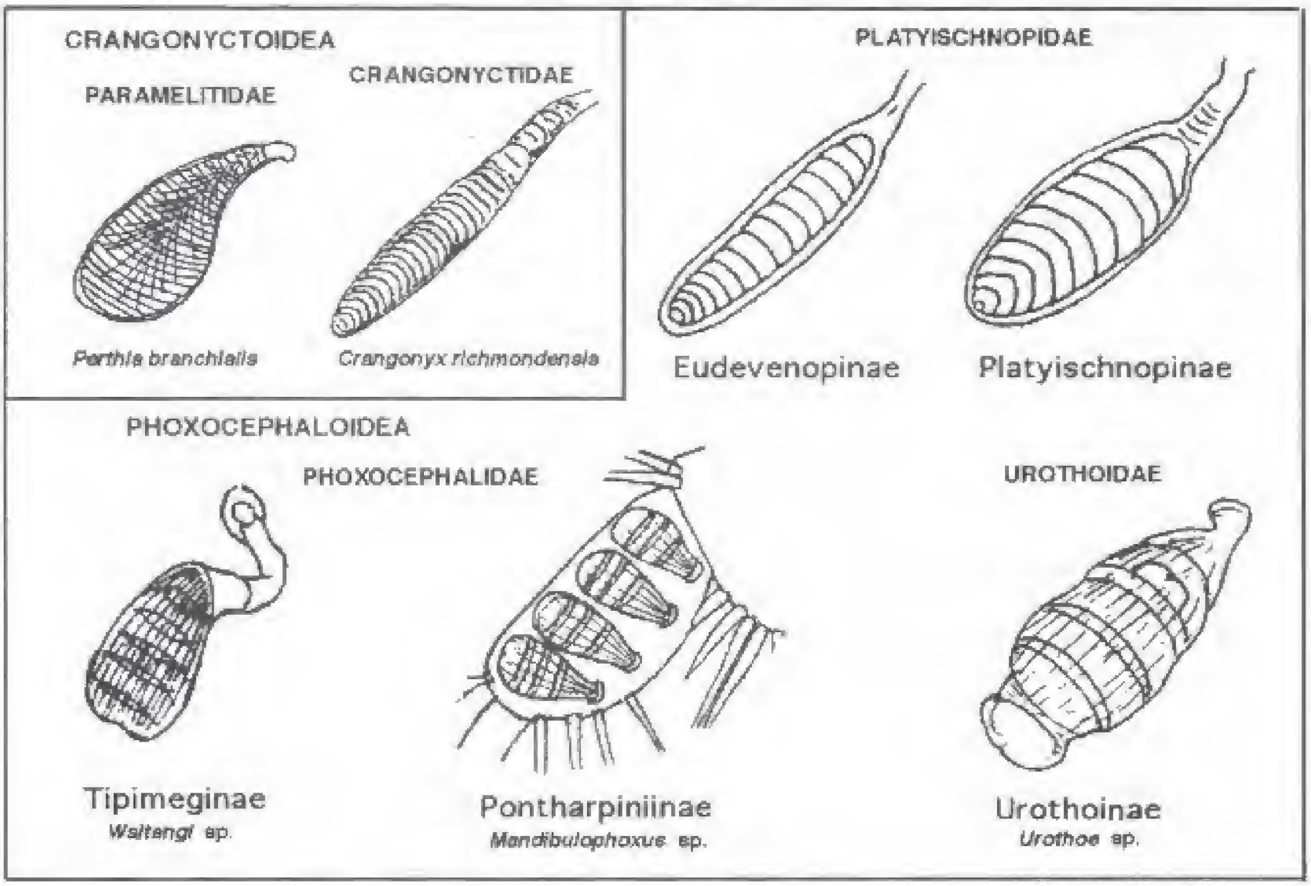


FIG. 10. PLESIOMORPHIC CALCEOLI: REPRESENTATIVE SUPERFAMILIES AND FAMILIES [after Jarrett & Bousfield, (1994 a, b), Godfrey et al (1988), and other sources]

on the vertical axis. The vertical and horizontal axes also simulate, fanwise, an approximate evolutionary time scale for the probable first appearance of the ancestral type of each major taxonomic group.

In this tentative scheme, the arrangement is rooted in a presumed mysid-like out-group in which calceolus-like structures were possible (cf. *Xenacanthomysis*; Fig. 9), at least on antenna 1 of the male. Such structures very probably occurred in presumed former epigean and pelagic marine ancestors of the now hypogean relict suborder Ingolfiellidea, and of the continental freshwater-endemic Crangonyctoidea. Such epigean and marine ancestral types have not yet been found extant, or in the fossil record, but are predicted from this study and from earlier considerations (e.g. Bousfield, 1982b). In this two-dimensional scheme, all members of the seven calceolate superfamilies, and the enigmatic (melphidippoidean?) hypogean calceolate *Sensonator valentiensis* Notenboom (1986), cannot be confined cleanly within any given graphical box. Such variance is attributable to parallel development, diversification, and subsequent loss of calceoli from the antenna of both sexes, presumably in response to changing life styles within the various taxonomic subgroups. Notably, the more strongly calceolate superfamily groups (calceoli on both A1 and A2, left column) are those in which members are primarily pelagic and/or mate freely in the water column. These include most of the Phoxocephaloidea, Pontoporeioidea, Lysianassoidea, Eusiroidea, and Oedicerotoidea. The less strongly calceolate superfamilies (with rare exceptions, calceoli on A2 only, right column) are found in the most primitive members of benthic superfamilies of the Reptantia, such as the Crangonyctoidea, and Gammaroidea. The position of acalceolate superfamilies is tentative, but is guided partly by the presence or absence of an antennal callynophore and other presumably primitive, often vestigial characters such as male antennal brush setae (see below).

With respect to the sexes, the more primitive types of calceoli occur (with very few exceptions) in the 'males only' category of presumed most primitive superfamily taxa such as the Crangonyctoidea, Phoxocephaloidea, Pontoporeioidea, and most of the Lysianassoidea (upper two rows). Calceolate females are frequent in pelagic (especially raptorial) members of Eusiroidea (e.g. Eusiridae and Gammarellidae), in some large hypogean predators in more primitve groups (e.g. *Crangonyx packardi, Sensonator*, p. 123), but rare in the fossorial Oedicerotidae, and benthic Gammaroidea.

With respect to calceolus morphology, the more advanced types occur mainly in the carnivorous family subgroups of the pelagic-mating Eusirioidea and Oedicerotoidea, and in the primitive benthic Gammaroidea (lower two rows).

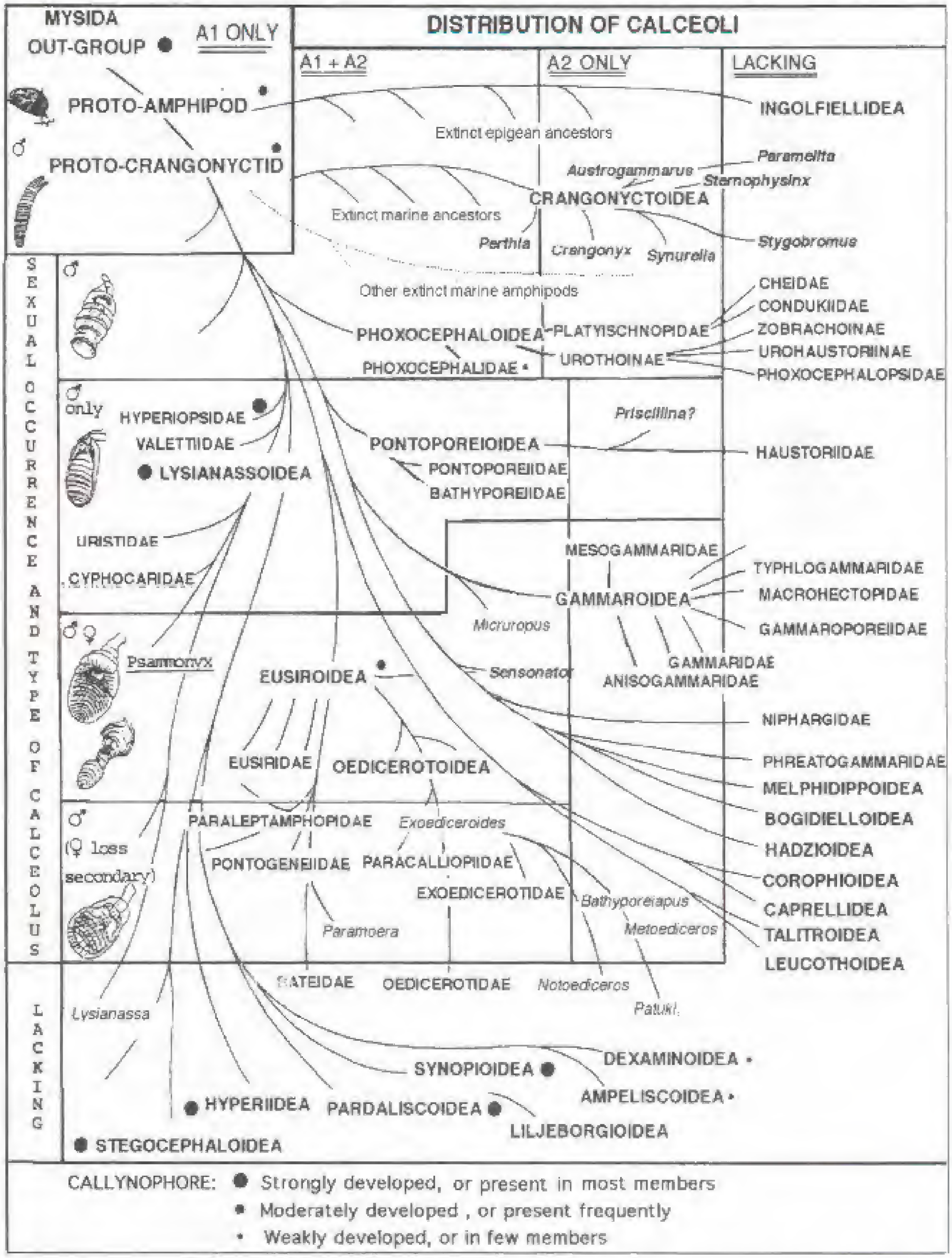


FIG. 11. PHYLOGENETIC RELATIONSHIPS WITHIN THE AMPHIPODA ACCORDING TO ANTENNAL DISTRIBUTION AND SEXUAL OCCURRENCE OF CALCEOLI.

These distributions suggest that calceoli developed initially (in males only) as a device presumably for detecting species-specific swimming vibrations of females at mating time. The calceoli became have become secondarily adapted, and more complex structurally (in free-swimming raptors), for detection of escape vibrations of free-swimming prey, and thus developed in females and immatures, as well as in reproductive males. As mating styles changed from pelagic to benthic and/or hypogean, lotic to lentic, marine to freshwater, involving pre-amplexus (see below), the primary rôle of calceoli correspondingly diminished or disappeared. The of reduction and disappearanceof calceoli from male antennae was apparently first from antenna 1, and then antenna 2; in the latter, the sequence was first from the peduncle, and finally from the flagellum. However, as noted above, calceoli persist (or become secondarily developed) in both males and females of some epigean (e.g., in some Anisogammaridae and Gammaridae) and/or cave pool amphipods (e.g. in *Crangonyx packardi* and *Sternophysinx calceola* of Crangonyctoidea; *Sensonator valentiensis* (Melphidippoidea?), and some large paraleptamphopid eusiroideans of New Zealand) (Bousfield, 1980) where life styles presumably remain free-swimming and raptorial.

Gnathod Structure and Phyletic Significance

Of all morphological characters of amphipod crustaceans, the gnathopods (peraeopods 1 & 2 of formal malacostracan terminology) have previously been considered one of the most significant and fundamental indicators of high level phyletic relationships, at least within the suborders Gammaridea (Stebbing, 1906; Barnard & Karaman, 1991); and Caprellidea (Laubitz, 1993; Takeuchi, 1993). Initially, and based on early taxonomic studies on intertidal groups of "good old Gammaridae" of northwestern Europe (J. H. Stock concept), the sexually dimorphic, powerfully subchelate form of the gnathopods, utilized in sexual precopulatory carrying behaviour in the male, was considered by many workers as the basic or ancestral amphipod reproductive form (e.g., Barnard, 1969a). More recently, however, extensive comparative morphological studies have been conducted on gnathopods and other phyletically significant characters (e.g. Bousfield, 1979a, 1982a, 1983, 1986), and the scope of their function in reproductive behaviour (e.g. Borowsky, 1984; Conlan, 1991a). These studies have correlated gnathopod morphology and sexual dimorphism, across a rather broad spectrum of amphipod superfamilies, with a pre-amplexing and/or mate-guarding form of reproductive behaviour. As summarized partly by Schram (1986), this form of reproductive behaviour is now considered by most workers as relatively highly evolved and specialized within the Amphipoda as a peracaridan group.

What then might be the probable ancestral form of the gnathopods, and concomitant ancestral reproductive life style within the Amphipoda? We might first look at gnathopod structure in members of various superfamilies that are classified as primitive on the basis of other plesiomorphic character states (per Bousfield 1979, 1983, etc.). The Lysianassoidea is one such superfamily group for which the distal portions of gnathopods 1 & 2 of species representative of the more primitive component families (Valettiidae and Uristidae) are detailed in Fig. 12 . In the very primitive genus *Valettiopsis* Holmes (see Barnard and Ingram, 1990), the carpus and propod of both gnathopods (in both sexes) are subsimilar, moderately slender and elongate, each with subparallel anterior (upper) and posterior (lower) margins. The propod is weakly but normally subchelate, the dactyl short and closely fitting the slightly oblique palm. In the slightly more specialized genus *Hirondella* , the carpus of gnathopod 1 is relatively short and shallowly lobate below. The propod is slightly narrowed distally, with an excavate palm, overlapped by the tip of the dactyl. In gnathopod 2, the propod is relatively short, and the palm slightly oblique forwards (parachelate). In the genus *Ventiella* , gnathopod 1 is little different, but in gnathopod 2, the propod has become much shortened, and the palm and dactyl much reduced in size to form a micro-subchela that is typical of the more advanced families and genera within Lysianassoidea. Within *Orchomenella* (family Uristidae), in addition to the micro-subchelate form of gnathopod 2, gnathopod 1 has also become structurally modified in having a much shortened carpus, with relatively narrow and deep posterior lobe, and the propod has become broadened, and the palm and dactyl enlarged and slightly parachelate.

In summary, despite minor modifications within an increasingly sophisticated generic series, we may note that the plesiomorphic form of both gnathopods may be described as non sexually dimorphic and weakly subchelate, with slender carpus and propod. Within the Lysianassoidea, characterized by gnathopods of the above type, mating takes place freely and rapidly in the water column, and there is no pre-amplexus or mate-guarding phase.

Gnathopods within Natantia.

If we examine a much broader range of superfamilies in which reproductive or mating style is free within the water column, and the taxa are relegated to the subgroup Natantia, a correspondingly broad range of gnathopod types can be identified (Figs. 12, 13). Within the primitive fossorial Phoxocephaloidea, gnathopod types range from the basically plesiomorphic form outlined in the Lysianassoidea (above), to a eusiroidean form with powerfully sub- or parachelate propod and dactyl, and slender posteriorly lobate carpal wrist. In some specialized lysianassids (hyperiopsids), eusiroideans (leptamphopids), stegocephaloideans, pardaliscoideans, synopioideans, dexaminoideans (lepechinellids), ampeliscoideans, and some melphidippoideans (Melphidippidae), the carpus and propod (of both gnathopods) may be secondarily abnormally elongated and slender. In others, especially the highly modified and specialized members of the fossorial, micro-carnivorous family Oedicerotidae, the gnathopods are raptorial or fossorial, but typically unlike in form, and the carpus is often much

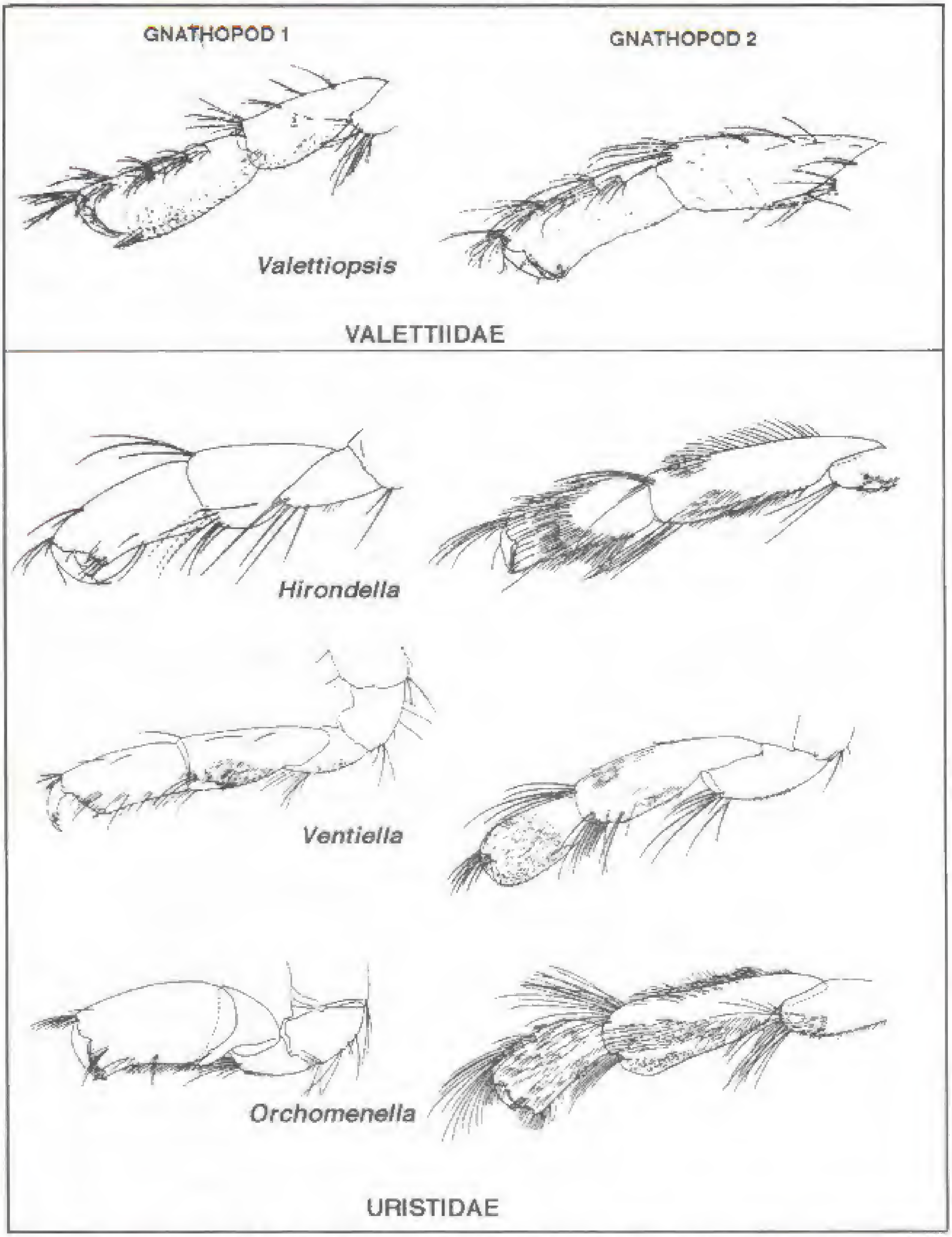


FIG. 12. FORM OF GNATHOPODS 1 & 2 IN LYSIANASSOIDEA
[after Barnard & Ingram (1990) and other sources]

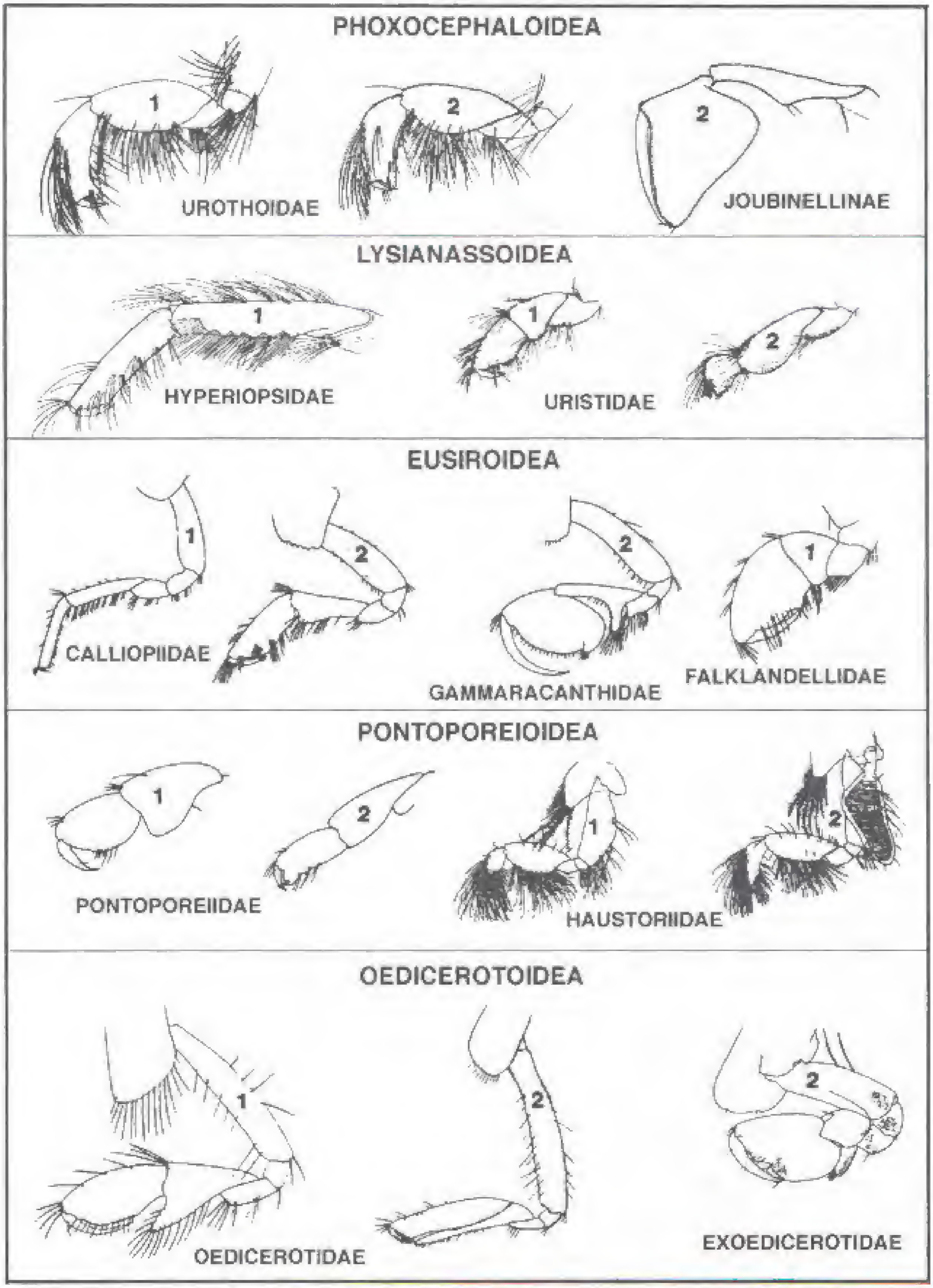


FIG. 13. FORM OF GNATHOPODS 1 & 2 IN SUPERFAMILIES OF AMPHIPODA NATANTIA (from various sources)

shortened and strongly produced posteriorly, the entire appendage functioning perhaps as a digging tool, as well as a raptorial chela. In hyperiids, the gnathopods are usually short and simple, nearly alike in form, and may serve mainly as accessory mouthparts (maxillipeds, as in decapod crustaceans). In the examples above, and in nearly all component family members of those superfamilies, the gnathopods are non- sexually dimorphic.

However, exceptions to this general trend within the Natantia are noted here. Thus within the vegetatively fossorial family Pontoporeiidae, although the reproductive style is pelagic and free within the water column, the gnathopods are also weakly but distinctly sexually dimorphic (see also Bousfield, 1987). Such a morphological anomaly may be vestigial, and represent a clue to phyletic relationships with other superfamilies such as the Gammaroidea. Thus, in such a scenario, we may presume a non-fossorial and pelagic common ancestor to both groups. However, in order to exploit food resources of physically harsh, lotic, intertidal, estuarine and fresh-water habitats, the ancestor may have become secondarily reproductively benthic, and developed weakly sexually dimorphic gnathopods and pre-amplexing mating behaviour. Today, its descendents that developed even more strongly sexually dimorphic and pre-amplexing gnathopods (i.e. now within the Gammaroidea) are widespread and highly successful in those physically rigorous habitats. By contrast, those that became fossorial in bottom sediments (i.e. now within the Pontoporeiidae) are today confined to lentic, lacustrine, or subtidal habitats within those environments that are still accessible to non-preamplexing reproductive life styles. In another evolutionary direction within that same superfamily, members of family Haustoriidae are characterized by weakly subchelate, non-amplexing gnathopods, yet almost certainly mate directly on or within the bottom sediments, not in the water column.

A parallel set of life styles and morphologies mark the Cheidae and most genera of Urothoidae within the austral fossorial counterpart superfamily Phoxocephaloidea. This phenomenon of superficial similarity has been demonstrated as an example of convergent or homoplasious evolution in otherwise phyletically very distant groups (see Bousfield, 1989), rather than an indicator of close natural relationships as proposed by Barnard and Drummond (1982) and maintained by Barnard & Karaman (1991).

Weakly sexually dimorphic gnathopods are also typical of some Dexaminoidea, and most of the Melphidippoidea (including the fossorial Megaluropidae). On the basis of other character states, and of some earlier field observations (e.g. of Enequist, 1950), members of both superfamilies presumably mate freely within the water column. However, many members within these groups are nestlers, commensals, or otherwise in the process of penetrating shallow-water, especially of anchialine brackish habitats of tropical and warm-water regions, where a pre-amplexing reproductive life style is likely advantageous. In a similar scenario, in which phyletic relationships are sought, we can reasonably look to a common ancestor for the Dexaminoidea and for the fossorial Ampelicoidea in which the gnathopods are non sexually dimorphic. However, the morphological specializations and tube-building capabilities of the fossorial ampeliscoideans have resulted in their enormously successful diversification and dominance in marine sedimentary habitats, even becoming major food items for eschrictid baleen whales. The presumed para-ancestral Dexaminoidea, however, are common in gondwanian regions (e.g. Australian coastal waters) but are now relatively rare and virtually relict in shelf habitats of the northern hemisphere (Bousfield & Kendall, 1994).

Within the Melphidippoidea, sexual dimorphism of the gnathopods is weakly to moderately strongly expressed, but is distinctly present in all members. It is also characterized (in the male) by a consistent similarity in appearance of gnathopods 1 & 2, although these differ markedly (between themselves) in size and form (Fig.14, bottom). These gnathopod characteristics are found elsewhere widely within the Hadzioidea (especially in the Melitidae) that are now much more widespread in tropical and temperate, coastal marine and brackish habitats. In combination with other character states (e.g. of the antennae, uropods, and telson, etc.), these gnathopod similarities may be extended, perhaps less strongly, to the Phreatogammaridae of brackish and fresh waters of New Zealand (e.g. in Bousfield and Ruffo, unpublished), possibly even to the hypogean brackish- and fresh-water Bogidielloidea, and even to Notenboom's (1986) remarkable, hypogean (but calceolate) *Sensonator*. In this vein, we are left with the exciting possibility, requiring much further investigation however, that present members of the marine and semi-relict superfamily Melphidippoidea are close to a postulated common ancestor to all of the above taxonomic groups (see phylogenetic tree, p. 126).

Finally, we may note within the group of superfamilies of Natantia, sexual dimorphism weakly expressed in gnathopods of certain austral freshwater members within certain freshwater members of superfamily Eusiroidea, but more strongly expressed within fresh and brackish water members of Exoedicerotidae and Paracalliopiidae (see also Bousfield, 1983). The freshwater eusiroidean species of *Falklandella* Schellenberg, 1931, and *Praefalklandella* Stock & Platvoet, 1991 (as in counterpart AZAC species of *Paraleptamphopus*) are characterized by a dominant gnathopod 1 that is weakly sexually dimorphic, and may have a pre-amplexing function. However, peraeopod 3 of *Falklandella* is also strongly sexually dimorphic, being carpochelate in the male (as in some species of *Paramelita* (Crangonyctoidea) and in many aquatic asellid isopods). This latter appendage may function in pre-amplexus, as it does in the isopods, but pertinent behavioural studies have not yet been made on these remote and presumably relict freshwater amphipod groups. In the antipodean oedicerotid families (above), the gnathopds are typically strongly sexually dimorphic, with gnathopod 2 dominant in males. A pre-amplexing carrying

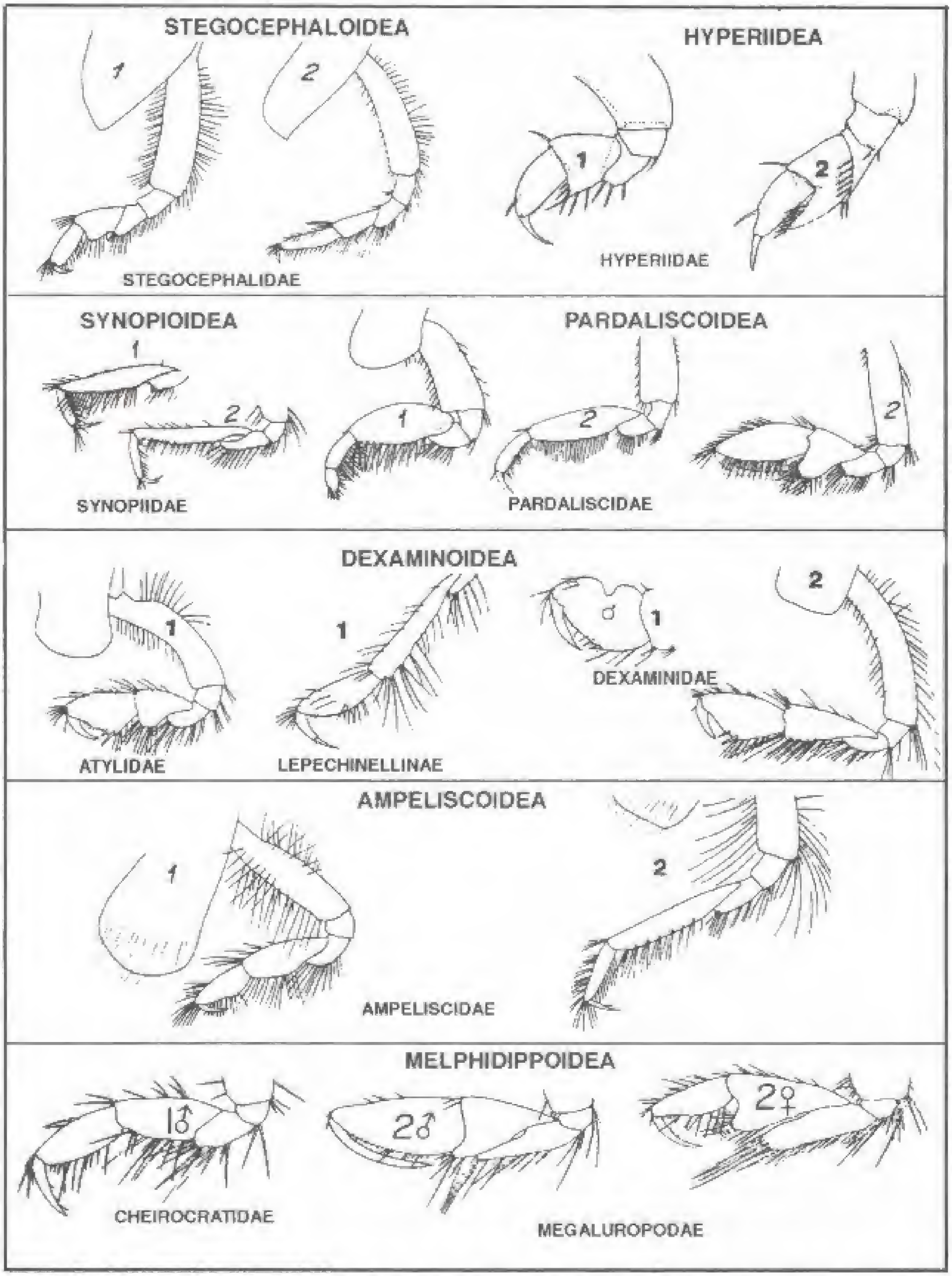


FIG. 14. FURTHER FORMS OF GNATHOPODS 1 & 2 IN SUPERFAMILIES OF AMPHIPODA NATANTIA (from various sources)

of females by males is typical (Chapman & Lewis, 1976; personal observation). Members of these two fossorial amphipod families are almost entirely intertidal, estuarine and fresh-water in their ecological affinities. Their form of gnathopod morphology, and pre-amplexing benthic reproductive behaviour is typical of the Reptantia. Within a superfamily of Natantia, these characteristics have virtually certainly been independently derived and are homoplasious with the condition in their gammaroidean taxonomic and ecological counterparts of the northern hemisphere.

We may conclude therefore that amphipod superfamilies herewith grouped within the category Natantia are typified by pelagic reproductive (mating) behaviour, and by non-sexually dimorphic gnathopods that are primitively weakly subchelate and subsimilar in form. A few subgroups within certain natant superfamilies evince a more reptant form of reproductive behaviour and gnathopod morphology. These exceptional instances can be explained, at least tentatively, on the basis of (1) a secondary use of sedimentary benthic substrata as a "fluid" mating medium wherein sexually dimorphic gnathopods and pre-amplexing mating behaviour may not be required (e.g. in Haustoriidae; Cheidae, Urohaustoriidae);(2) an independent or convergent evolution within geographically isolated sub-taxa that have been exposed to similar, mainly ecological, evolutionary stresses (e.g. southern families of Oedicerotoidea); (3) a morphology vestige of presumed ancestral types whose evolutionary "thrust" devolved mainly into other super-family groups that are, today, essentially "reptant" in reproductive life style (e.g. in Pontoporeiidae); or (4) a probable extant precursor of more successful (biogeographically and ecologically more widespread and diverse) descendent modern taxonomic groups (e.g. in Dexaminoidea, Melphidippoidea).

Gnathopod structure and function in "Reptantia"

The types of gnathopods representative of component superfamilies of the reproductively benthic and/or pre-amplexing category Reptantia are illustrated in Figs. 15, 16, 17, & 18. Within Reptantia, gnathopod morphology is basically different, and the range of morphotypes is considerably greater, than that already demonstrated in the Natantia (above). Thus, in most superfamilies of Reptantia the gnathopods are characteristically sexually dimorphic and strongly subchelate or cheliform, especially in males. However, many exceptions to these overall trends have been noted, and are hopefully plausibly accounted for, in the discourse below.

In phyletically more primitive superfamilies (so determined from previous studies and from other character states above) such as the continental freshwater Crangonyctoidea and the holarctic fresh- and brackish-water Gammaroidea (Fig. 10), the gnathopods are variously (usually markedly) sexually dimorphic, with gnathopod 2 usually "dominant". In Crangonyctoidea (as in Natantia), the mature male stage (usually calceolate) is terminal (or subterminal, fide Conlan), as in most Natantia. Precopulatory carrying of the female by the male is not documented, although it is suspected to occur in epigean members of the Paramelitidae (e.g. in *Paramelita*, and *Austrogammarus*), where males are distinctly larger than females. In the holarctic family Crangonyctidae, whose members (especially hypogean species) appear to be mainly raptors, gnathopods of both males and females are often quite large and powerful. However, males are typically much the smaller of the two sexes and presumably physically incapable of carrying females. In true amplexus, the male first gnathopods are used to grasp the female laterally by the coxal plates, and the second gnathopods remain free, presumable to fend off other males (personal observation; Conlan communic.).

In most Gammaroidea, however, males are typically larger and more powerful than females, and pre-copulatory carrying is the reproductive norm. In family Gammaridae, the first gnathopods typically have a very oblique palmar margin, enabling the pair to be employed in a "fore-and-aft" seizing of the first and fifth peraeonal (body) plates of the female. The larger second gnathopod are employed in agonistic behav-iour to other males (and occasionally in carnivory of newly moulted female of their own and other species!) (Borowsky, 1984; Costello, 1993, this symposium). Within family Anisogammaridae, the palm of gnathopod 1 is vertical, studded with "peg-spines", and presumably better suited to lateral grasping of the anterior margin of coxal plate 4 than peraeonal plates (Bousfield, 1986, pers. observation (in *Eogammarus*).

Within the Talitroidea (Fig. 16) pre-amplexus is typical of the intertidal and brackish-water family Hyalidae, the intertidal fossorial Dogielinotidae, the coastal marine and fresh-water Hyalellidae, and the more primitive members of the supratidal family Talitridae. The gnathopods are strongly sexually dimorphic, and in the usually larger male, gnathopod 2 is especially powerfully subchelate, probably for use in agonistic display, and in fending off other males. In carrying activity within most Hyalidae, Hyalellidae, and Dogielinotidae, gnathopod 1 is modified to grasp the margin of a special pre-copulatory notch in the antero-ventral margin of peraeon 2 of the receptive female (see Borowsky, 1984; Bousfield 1986, 1993). However, in the most terrestrial landhopper groups (Bousfield, 1984, 1988), in the most specialized aquatic inquilinous families (e.g. Eophliantidae), and in the kelp-borers (Najnidae), the gnathopods are weakly (or not) sexually dimorphic, and pre-amplexus is lacking, apparently lost secondarily.

Within the Hadzioidea (especially family Melitidae)(Fig. 17), gnathopods are typically strongly sexually dimorphic, and pre-amplexing reproductive style prominent in all but the most hypogean subgroups. Using gnathopod 1, the propod and dactyl of which may be specially modified to clasp the female by an antero-ventral process of coxa 6 (in *Abludomelita* and relatives)(Borowsky, 1984, Bousfield, pers. observation). The much larger male gnathopod 2 is held freely, and functions in agonistic behaviour toward other males. In the tropical and warm-temperate marine

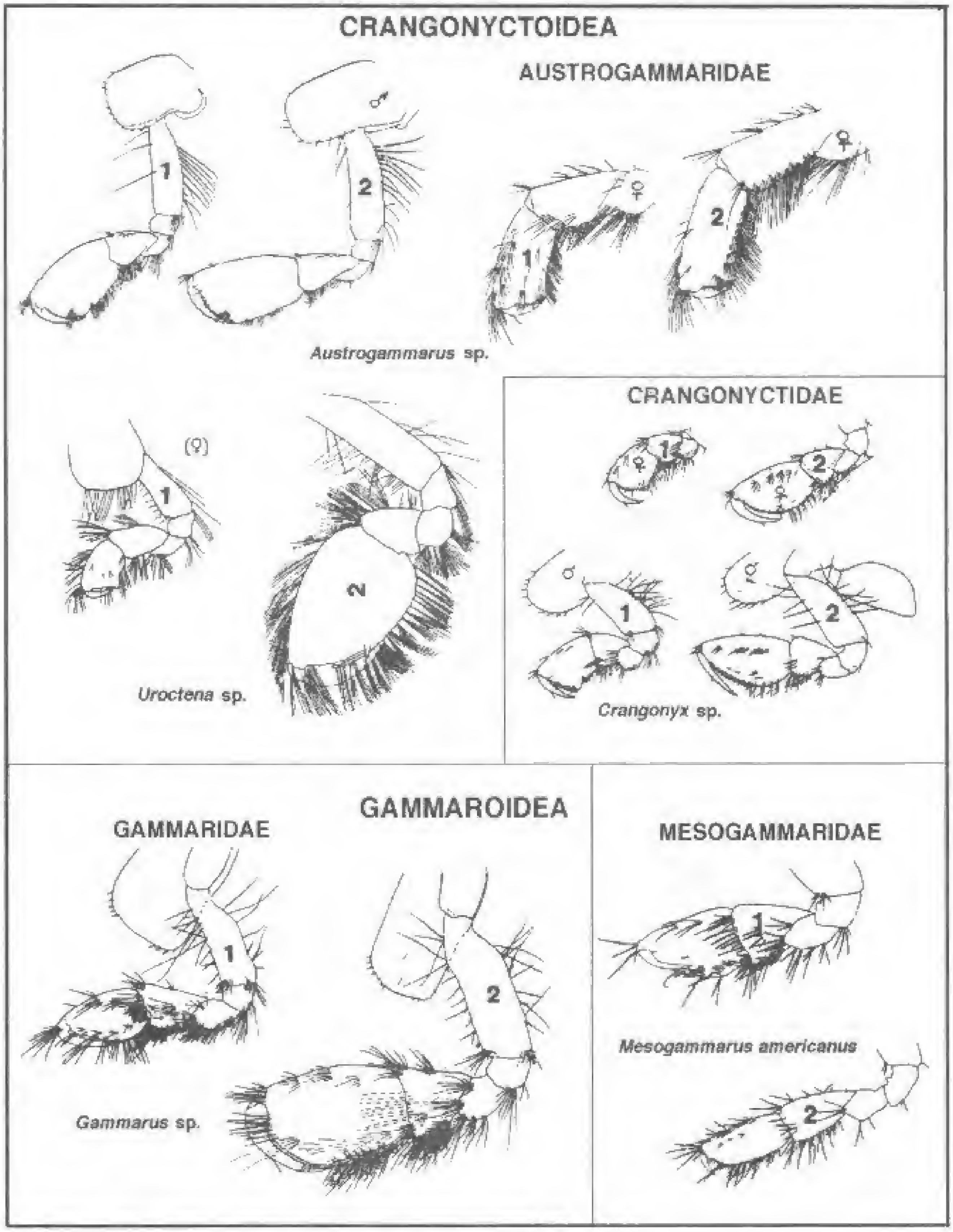


FIG. 15. GNATHOPODS 1 & 2 IN PRIMITIVE SUPERFAMILIES OF AMPHIPODA REPTANTIA [after Bousfield (1958; 1979) and other sources]

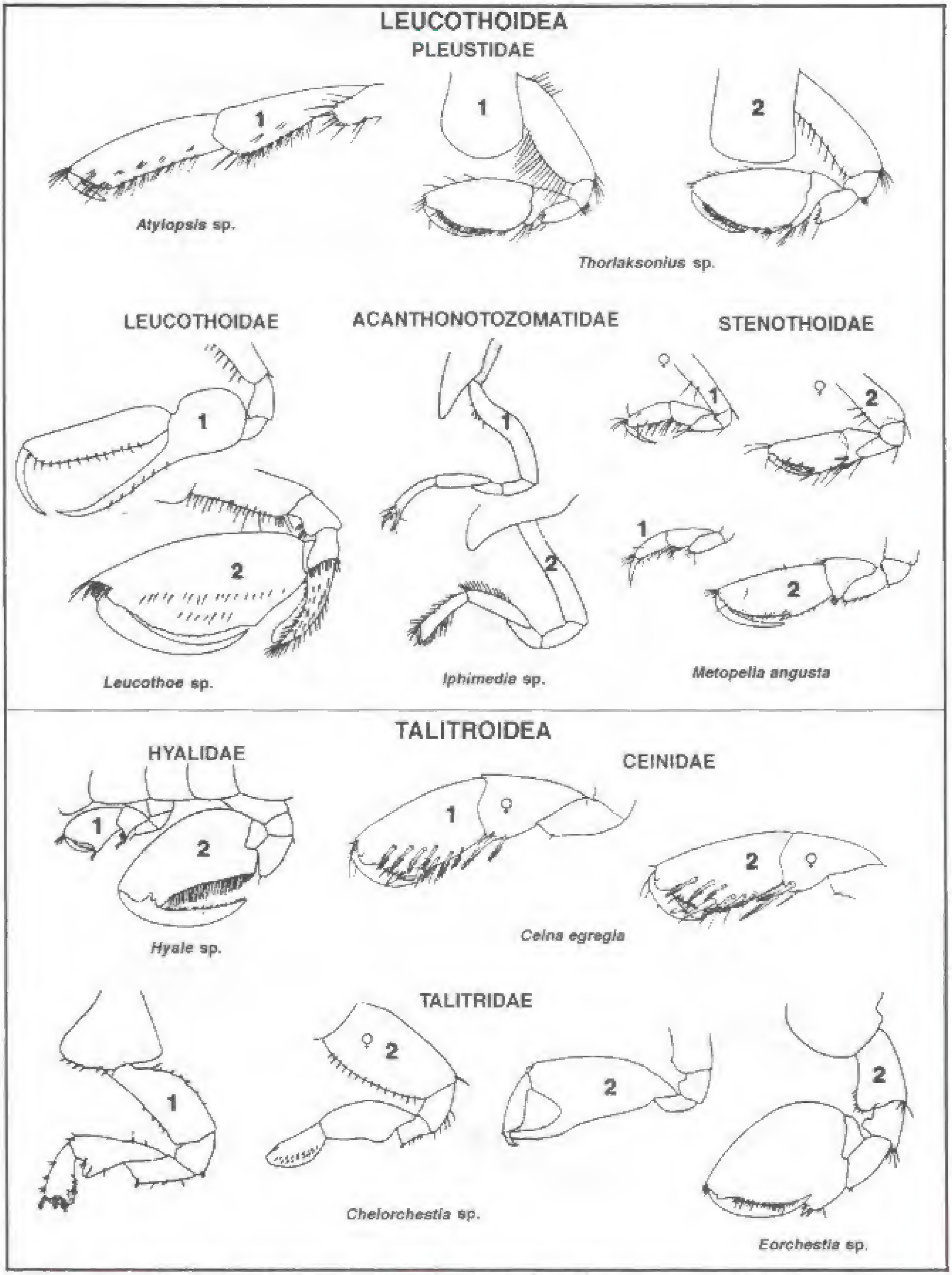


FIG. 16. GNATHOPODS 1 & 2 IN MEDIUM ADVANCED SUPERFAMILIES OF AMPHIPODA REPTANTIA [All males except where indicated] (from various sources)

genus *Dulichiella*, either the right or left gnathopod 2 of the male is enormously developed (Fig. 17). The dactyl is greatly enlarged, and its tip fits into a socket in the antero-ventrally produced palmar angle of the propod. Its overall form is grossly similar to the morphology of the gnathopod of the decapod "snapping shrimp" (genus *Alphaeus*?) suggesting that it functions in percussive sound production, either to attract receptive females or to warn away other males. However, in most of the hypogean hadzioideans (e.g. weckelids, metaniphargids, metacrangonyctids, etc.), whether the gnathopods are strongly or weakly raptorial, sexual dimorphism is weak or lacking (Stock, 1985; Holsinger, 1992b).

Within the tube-building Corophioidea occurs perhaps the greatest range of gnathopod sexual dimorphism of any reptant amphipod superfamily (Fig. 18). In the male, the gnathopods are typically strongly subchelate or carpochelate, but very unlike in form and size. The second gnathopods are usually very much the larger, more complex, and dominant, except in the Aoridae and Cheluridae where gnathopod1 is the larger. Since corophioideans are sequestered in open-ended tubes of their own construction, they have become, effectively, semi-sessile, and stray little from a fixed location. Such a life style may have resulted in secondary loss of precopulatory "carrying" of the female. Instead, the male "guards" the female in her tube and employs the enlarged gnathopod 2 mainly in agnostic behaviour towards competing males who might approach his reproductive territory (Borowsky, 1984, Conlan, 1988, 1991a). However, pre-amplexus is retained in the free-clinging family Podoceridae and in the presumed descendent Caprellidea, (including Cyamidae) in nearly all species of which the gnathopods are var iously strongly sexually dimorphic (see Laubitz, 1970, 1979, 1993); Takeuchi, 1993).

Across the reptant classificatory board, however, some important exceptions to this general picture should be noted. Within the relatively plesiomorphic reptant superfamily Liljeborgioidea (Fig 17, top), sexual dimorphism of the gnathopods is most strongly pronounced in the free-living families Liljeborgiidae, Sebidae, and the sponge-dwelling Colomastigidae, but is weak or virtually non-existent within the hypogean Salentinellidae and Paracrangonyctidae. Within other hypogean superfamily groups, especially those believed to be micro-predators (e.g. Bogidielloidea, Ingolfiellidea), the gnathopods are powerfully subchelate or carpochelate and raptorial, but appear weakly (or not) sexual dimorphic. Finally, within the diverse and possibly polyphyletic assemblage of families currently assigned to the exclusively marine superfamily Leucothoidea, a correspondingly immense diversity of gnathopod types may be seen. Gnathopods 1 & 2 are often much enlarged and of unusual or bizarre form, and often very different from each other in form and size. Taxa within families Leucothoidae, Amphilochidae, and Pleustidae, etc., whose vegetative life styles are commensal, inquilinous, or parasitic, exhibit virtually no sexual dimorphism of the gnathopods. However, in free-living groups such as the Stenothoidae and some of the Pleustidae, especially those of intertidal and brackish habitats (e.g. "*Parapleustes*" *den*), the gnathopods are variously (often strongly) sexually dimorphic.

In summary, within component superfamilies of Reptantia, we may conclude that sexual dimorphism of the gnathopods, and benthic pre-amplexing reproductive styles are dominant and characteristic of member groups that are vegetatively free-living and epigean in physically rigorous habitats such as coastal shallows, estuaries, and fresh-waters. Conversely, in members that have become (presumably secondarily) symbiotically associated with other animals or plants of marine environments, or penetrated into hypogean brackish- and fresh-water, or fully terrestrial habitats, sexual dimorphism of the gnathopods is expressed weakly or not at all. As a group, the reptants include the most derived amphipod morphotypes, that exploit unusual or restricted food resources under physically rigorous or unusually specialized environmental conditions. In the corresponding reproductive evolutionary sequence, a pre-amplexing reproductive (mating) style is presumed to be an effective means of ensuring species continuity. Thus, at the precise time of ovulation during the female moult cycle, the newly laid eggs (within the female brood pouch) must be fertilized by the male. Without the ensured presence of the male at that time the species could not remain in place within the specialized habitat nor remain viable as a species. However, where such a mechanism is no longer needed to ensure such close contact (as in lentic hypogean habitats, or under confined symbiotic conditions), or the carrying mechanism become physically impossible to maintain (as in terrestrial habitats), the gnathopods lose (presumably secondarily) the sexually dimorphic form, and neotenically revert to a morphology suited to the vegetative life style of both sexually mature adults and immature stages.

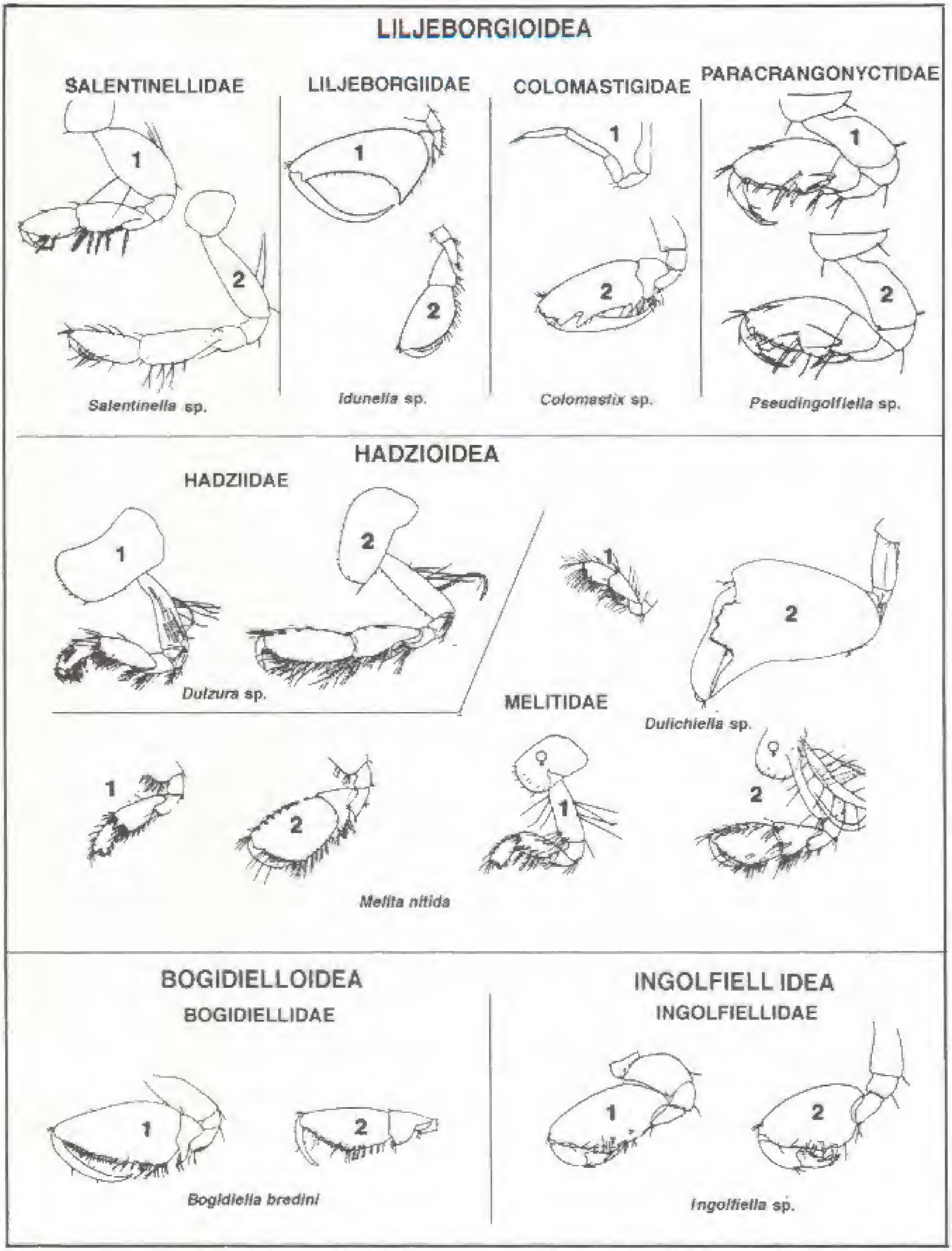


FIG. 17. GNATHOPODS 1 & 2 IN ADVANCED SUPERFAMILIES OF AMPHIPOD REPTANTIA [Males unless specified] (from several sources)

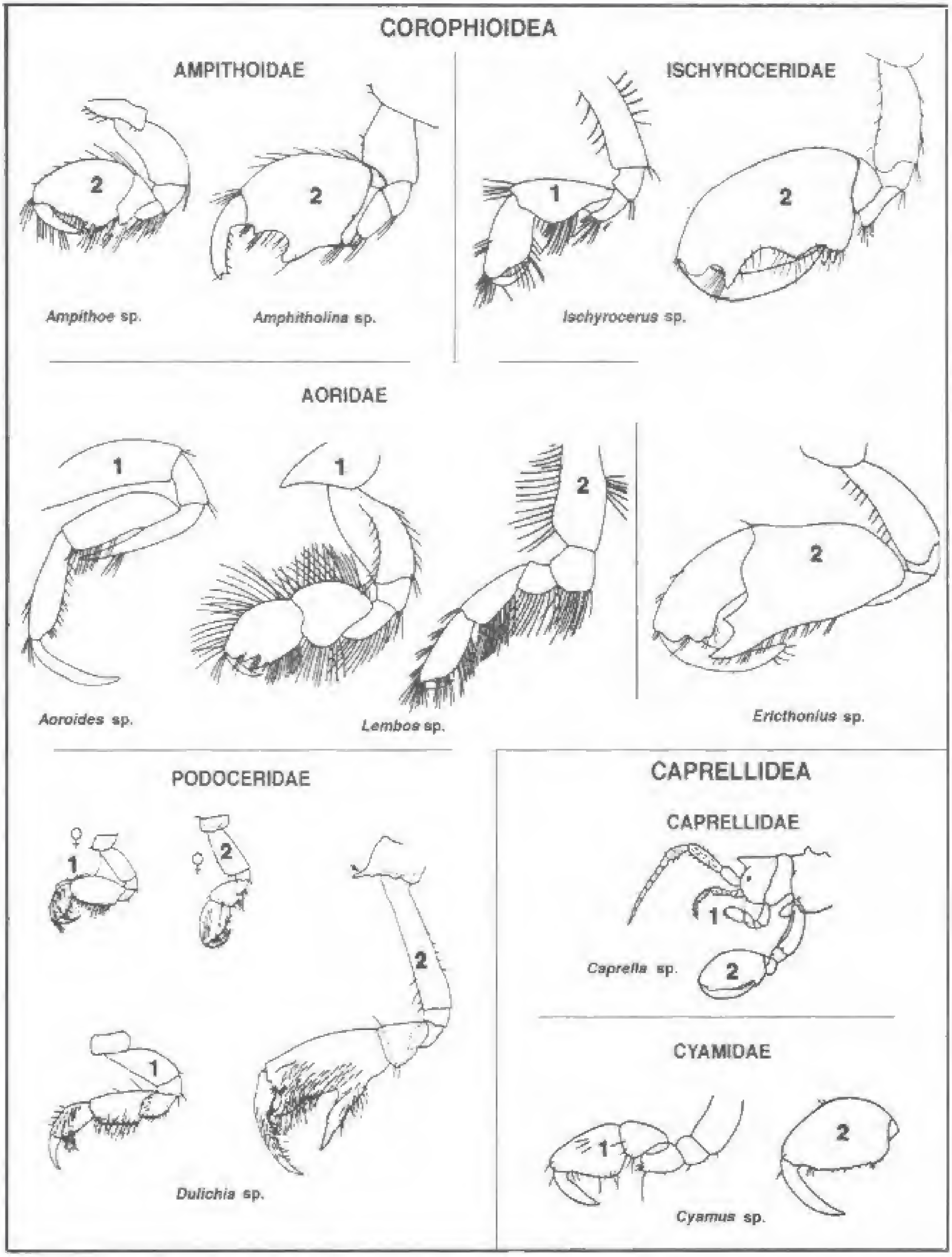


FIG. 18. GNATHOPODS 1 & 2 IN COROPHIOIDEAN AND CAPRELLIDAN AMPHIPODA [males unless specified] (from several sources)

Mating Behaviour Within the Amphipoda

Conlan (1991) has summarized recent advances in work on the significance of precopulatory mating behaviour and sexual dimorphism in phyletic relationships of amphipod crustaceans. Amphipods employ two basic reproductive strategies to ensure proximity of males and females at the time of female ovulating ecdysis:

(1) mate-guarding, in which the males are either (a) carriers involving pre-amplexing and concomitant modification of male gnathopods for the purpose, or (b) attenders, where they remain domiciled with the female and employ the gnathopods mainly in agonistic manner to ward off competing males.

(2) non-mate-guarding in which the mature male simply seeks out females wherever they may be at the time of ovulation. These males are classified as (a) pelagic searchers if the female is in the water column, or (b) benthic searchers if the female is on or in the bottom substrata. In either case the gnathopods are little or not sexually dimorphic, and no pre-amplexus takes place. Both strategies are determined by the period of ovulation of the female, at which time the male must be present if fertilization of the eggs is to take place. For a short period immediately following moulting, the cuticle of the female is sufficiently flexible to allow for release of the eggs into the brood pouch or marsupium. Sperm is deposited there by the male during copulation, and fertilization of the eggs can then take place.

Conlan (loc. cit.) has concluded that the searching strategy is a primitive, and mate-guarding an advanced, form of reproductive behaviour in amphipods. This conclusion provides the principal basis for present semi-phyletic classification of amphipod superfamilies (fig. 30, p.126).

In these mating strategies, the reproductive morphology of the mature female is seldom significantly different from that of the vegetative or feeding stages, except in some species of *Melita*, some aquatic talitroideans and a few others (see below). However, the breeding frequency and fecundity reflect overall differences in mating strategy. Thus, females of mate guarders tend to be iteroparous, with several broods in a life time, whereas those of non-mate-guarders tend to be semelparous, with only one brood in a life-time.

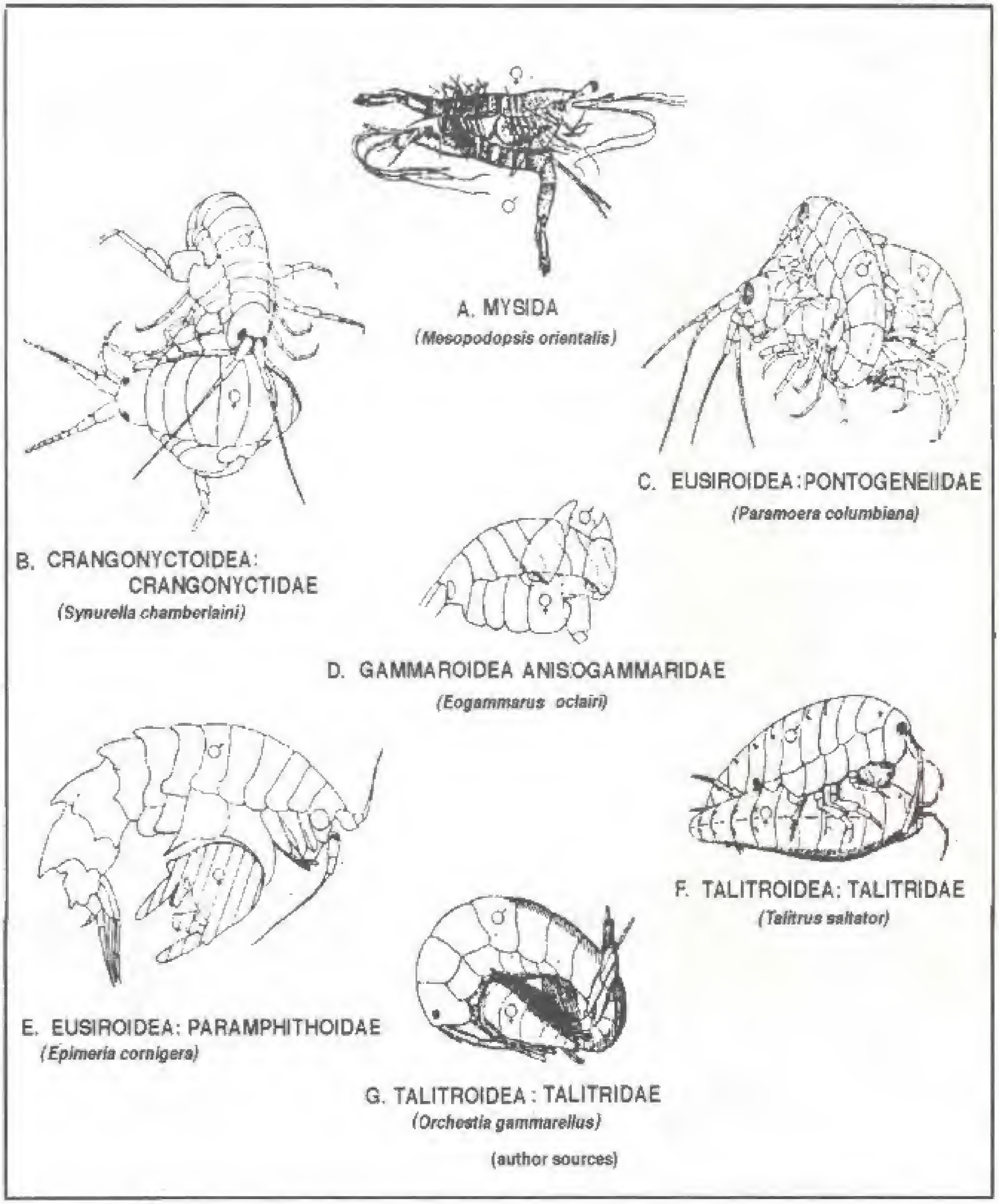
Examples of amplexus or copula within superfamilies of Amphipoda are illustrated in Fig. 19. Inset figures C and E are representative of superfamilies of Natantia; B, D, F, G, are representative of the Reptantia. For comparative purposes, the copulatory position of an outgroup mysid pair (*Mesopodopsis orientalis*) is included (from Nair, 1939). The ventral "head-to-tail" position of the male mysid permits direct access of the penis papillae to the posterior opening of the marsupium, and presumably facilitates temporary clasping of the female abdomen by the male peraeopods. The function of the modified and elongated pleopods 4 & 5 has not been described; their position beneath the anterior end of the female would suggest a tactile, rather than sperm-transfer role.

The mating position in amphipods contrasts with that in mysids except that, in both groups, the process is relatively rapid and takes place usually in darkness. In most superfamily groups within Natantia, contact between the mate-seeking male and the female takes place only during actual copulation, and its duration is brief (Conlan, 1991). In superfamily Eusiroidea, family Pontogeneidae, the smaller male of *Paramoera columbiana* lies across the thoracic region of the female, grasping her by the peraeonal and coxal plates "fore and aft", using both pairs of gnathopods. Within the benthic and less mobile members of the Paramphithoidae, the male of *Epimeria cornigera* holds the female crosswise under the specially curved lower margins of his coxal plates 4 & 5 (Moore, 1981), the gnathopods apparently playing little part in the action.

Within the Reptantia, and in the primitive superfamily Crangonyctoidea (e.g. *Synurella chamberlaini*), the smaller male grasps the female sidewise by the coxal plates, and inserts the dactyls of gnathopods 1 & 2 between the lower anterior margins of coxae 3 & 4 respectively. The paired antennae are pressed closely to the body of the female, with the calceoli nearly everywhere in contact with the female's body surface. In family Anisogammariae (Gammaroidea) the dorsally positioned male grasps the female by the anterior margin of coxal plates 4 & 5, using gnathopod 1 (Fig. 19D). In the semi-terrestrial Talitridae (Talitroidea), the male crouches across the female, lying on her side, and positions her by means of his gnathopods and the enlarged peduncles of antenna 2 working in concert (Fig. 19D).

Pre-amplexing positions are illustrated in Fig. 20. Preamplexing is rare within the superfamilies of Natantia, and where it does occur, briefly, differs little from amplexus (Fig. 19A). Within the Reptantia, however, pre-amplexus is nearly the rule. In the primitive Gammaroidea, males of Anisogammaridae (e.g. *Eogammarus oclairi*) carry the smaller female by grasping the base of coxa 4, usually by means of gnathopod 1. In *Gammarus* (family Gammaridae), the male carries the female by means of a "fore-and aft" clutching of the anterior edge of peraeon plate 1 and posterior edge of peraeon 5, using gnathopod 1, facilitiated by its very oblique palms. Within the Hadzioidea, the male of *Melita nitida* grasps the female by the specially modified anterior lobe of her coxa 6, using the smaller gnathopod 1 for the purpose. The much enlarged male gnathopod 2 may be used in fending off competing males. In many aquatic Talitroidea, especially in *Hyalella* and *Allorchestes* (Hyalellidae) and in *Hyale* and *Parallorchestes* (Hyalidae), the dorsally positioned male inserts the dactyl of gnathopod 1 in a precopulatory notch in the lower anterior margin of peraeon 2 of the smaller female. Again, the much enlarged gnathopod 2 apparently functions agonistically. In some species of *Hyale*, however, gnathopod 2 may be inserted into the female notch.

These reproductive strategies are basically similar at superfamily level but differ in detail internally. They do demonstrate the widespread phenomenon of convergent evolution of similar mating strategies, with differing tactics and morphologies at the family and subfamily levels.



A. MYSIDA
(*Mesopodopsis orientalis*)

B. CRANGONYCTOIDEA: CRANGONYCTIDAE
(*Synurella chamberlaini*)

C. EUSIROIDEA:PONTOGENEIIDAE
(*Paramoera columbiana*)

D. GAMMAROIDEA ANISOGAMMARIDAE
(*Eogammarus oclairi*)

E. EUSIROIDEA: PARAMPHITHOIDAE
(*Epimeria cornigera*)

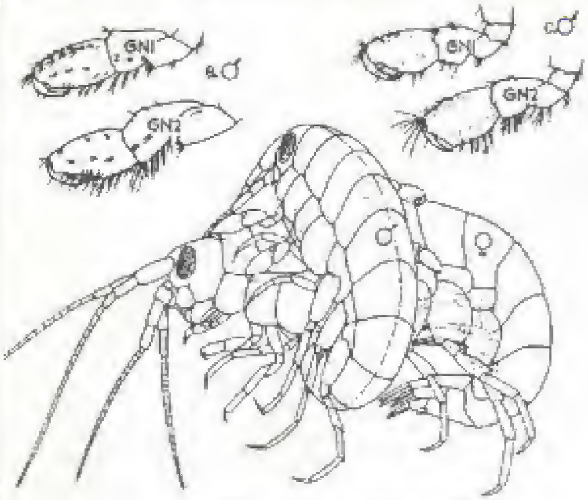
F. TALITROIDEA: TALITRIDAE
(*Talitrus saltator*)

G. TALITROIDEA : TALITRIDAE
(*Orchestia gammarellus*)

(author sources)

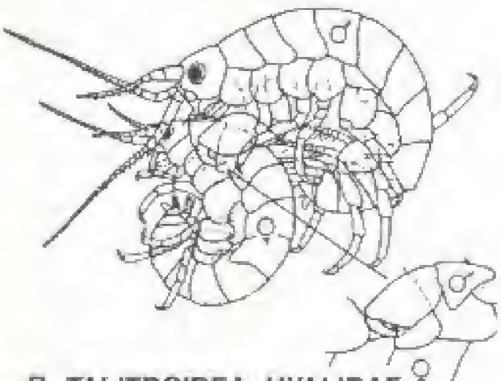
FIG. 19. AMPLEXING POSITIONS IN REPRESENTATIVE SUPERFAMILIES OF AMPHIPODA, AND MYSIDA

A. (after Nair, 1939) E. (after Moore, 1981) F. (after Williamson, 1951) G. (after Williamson, 1951) B. D. C. (authors sources)



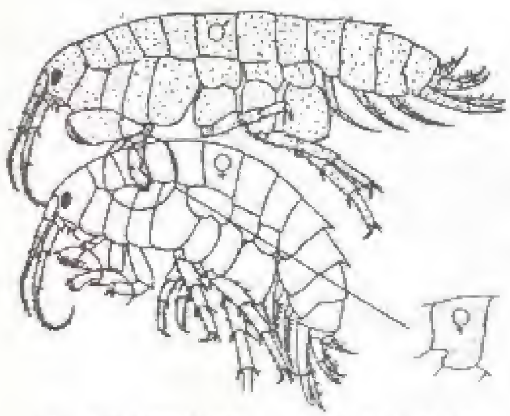
A. EUSIROIDEA: PONTOGENEIIDAE

(Paramoera columbiana)



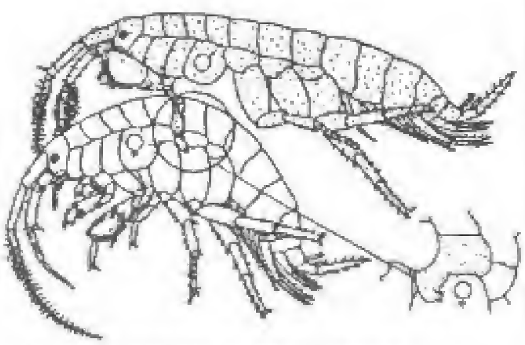
B. TALITROIDEA: HYALIDAE

(Hyale seticornis)



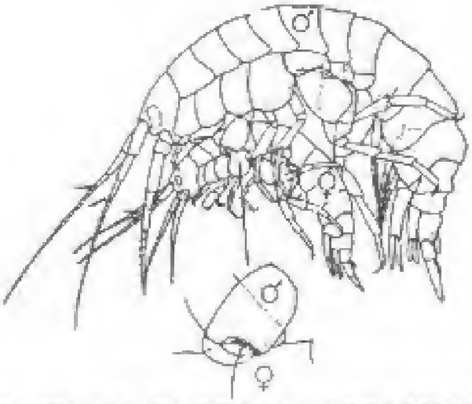
C. TALITROIDEA: HYALELLIDAE

(Hyalella azteca)



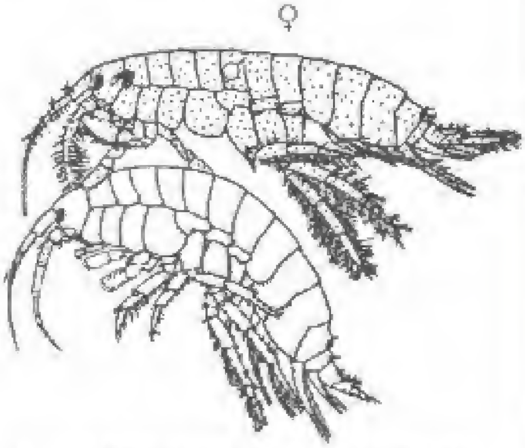
D. HADZIOIDEA: MELITIDAE

(Melita nitida)



E. GAMMAROIDEA: ANISOGAMMARIDAE

(Eogammarus oclairi)



F. GAMMAROIDEA: GAMMARIDAE

(Gammarus fasciatus)

FIG. 20. PRECOPULA IN REPRESENTATIVE SUPERFAMILIES OF AMPHIPODA "REPTANTIA" (after Borowsky (1984) and authors sources)

Phyletic Significant of Uropod 3.

The significance of uropod 3 in the general description and classification of amphipod crustaceans has always been primary (Stebbing, 1906; Gurjanova, 1951; Barnard, 1969a; Barnard and Karaman, 1991). Its character states have proven especially valuable in preparing taxonomic keys to regional and world faunas, at generic and family levels (e. g. Staude, 1987; Barnard & Barnard, 1983. Its rôle in phyletic and semi-phyletic classification of amphipods (except in some Corophioidea, and the Caprellidea where the abdomen is variously reduced and uropod 3 vestigial or lacking) has been considered previously (e.g. Lincoln, 1979; Bousfield, 1979a, 1982a, 1983; Bowman and Gruner, 1973). However, more detailed study of its form and function in relation to broader aspects of phyletic classification would seem fruitful, and therefore forms a principal part of this overview study.

In the Amphipoda, uropod 3 forms the terminal set of paired body appendages. It is distinguished from uropods 1 & 2 by its form and function. Uropod 3 is primarily a swimming appendage, whether functioning in propulsion or steering. The rami are typically broadened or flattened, and the margins lined with long plumose setae that provide a large surface area for effective paddling or steering action. Uropods 1 & 2 are used mainly in strengthening the caudal portion of the body to permit jumping or flipping, by rapid flexion of the urosome (Barnard & Karaman, 1991); they are secondarily modified for copulatory or tactile function in specialized habitats but are seldom modified for swimming.

The most plesiomorphic and generalized form of uropod 3 is typical of the Natantia and more primitive Reptantia (Figs. 21, 22 upper). The paired rami are large, lanceolate, and typically subequal in length (aequiramous condition), and the inner and outer margins variously lined with plumose setae and/or short spines (Figs. 21A-D). The terminal segment of the outer ramus is present (plesiomorphic condition) in the more primitive superfamilies such as the Phoxocephaloidea, Lysianassioidea, and Pardaliscoidea (Figs.21A-D), but trends to loss or fusion with the proximal segment in advanced callynophorates (e.g.Stegocephaloidea ,Fig. 21N, O) or in vegetatively benthic forms such as Pontoporeioidea (Fig. 21 G,H). In many pelagic groups (within Eusiroidea, Oedicerotoidea, Synpioidea, Hyperiidea, Melphidippoidea and pelagic males of Dexaminoidea and Ampeliscoidea), the terminal segment is totally lacking (Fig. 21E, F, L, M, P, Q, T, V, X). In more advanced, especially abyssal-benthic forms (e.g. Lepechinellinae), both rami may be reduced in size and swimming setae lost, or nearly so (Fig. 21 U).

Within the Natantia, especially the Pardaliscoidea, and Hyperiidea having a pelagic life style, sexual dimorphism of uropod 3 is generally slight, the rami being scarcely more strongly setose in the male than in the female. However, in vegetatively benthic and reproductively pelagic taxa such as Phoxocephaloidea and Pontoporeioidea, sexual dimorphism of uropod 3 is often pronounced. In female and immatures the appendage is much smaller, the inner ramus is often reduced in size (parviramus condition, Fig. 21B, J), and ramal margins usually lack swimming setae. Exceptionally, in some of the Pontoporeioidea (e.g. Haustoriidae) and many of the Oedicerotoidea (Oedicerotidae), mature males may be secondarily infaunal and/or mate within the substratum, and show little or no retention of the natatorial form of uropod 3 (Fig. 21K, L).

Apomorphic conditions of uropod 3 characterize the more advanced superfamily groups within the Reptantia (Fig. 22, lower, Fig. 23). Only within primitive crangonyctoideans, gammaroideans, hadziodeans and liljeborgioideans is the fully biramous and/or marginally setose condition encountered (Fig. 22A-F; Fig. 22L). In the hypogean Bogidielloidea, the rami remain essentially aequiramus and not sexually dimorphic, despite overall reduction in size, general lack of marginal setae, and loss of the terminal segment of the outer ramus (Fig. 22O, P). This feature suggests a close natural relationship of the Bogidielloidea to the epigean Melphidippoidea. In more advanced hypogean forms, the terminal segment of the outer ramus may be much enlarged and especially distinctive in males (as in *Eriopisa* Fig. 22H, *Ginniphargus* (Williams and Barnard, 1988), in several species of *Allocrangonyx* and *Pseudoniphargus* and in many Niphargidae (Barnard & Barnard, 1983). In these forms, the primary function may be tactile, as in the elongate antennae and elongate, setose peraeopods. More often, however, one or both rami are reduced, often markedly so, with total loss of marginal setae, and/or spines, as in infaunal or hypogean crangonyctoideans, hadzioideans, gammaroideans and liljeborgioideans (Fig. 22E, G, J, K, M, N).

Within Amphipoda Reptantia, sexual dimorphism of uropod 3 is variously expressed, often strongly so, depending to large degree on reproductive life style. In primarily benthic taxa, with pre-amplexing or benthic reproductive style, uropod 3 is moderately sexually dimorphic in freely ambulatory groups, both epigean and hypogean (e.g. in primitive Crangonyctoidea and Gammaroidea, less so in primitive Hadzioidea and marine Liljeborgioidea). In groups that have apparently become secondarily aquatic (non terrestrial Talitroidea), the rami have are very short, vestigial or lacking (Fig. 23D, E). Sexual dimorphism of uropods is entirely lost (or nearly so) in tube-building, inquilinous, commensal, advanced hypogean, and saltatory groups (e.g. most Corophioidea, Leucothoidea, Liljeborgioidea, and Talitroidea). Here the appendage is often highly modified or specialized, in both form and function, in both sexes (Fig.23A, B, C). Within the domicolous Corophioidea, uropod 3 is much reduced, with rami typically short and slender, but remains biramous (even with terminal segment of outer ramus in some primitive Iscaeidae) in all but the most advanced Aoridae and Corophiidae (Fig. 23H, J). In the Ampithoidae and Ischyroceridae, the outer ramus is equipped distally with hooks and spines for the purpose of retaining hold of its tube while foraging from the entrance or repelling invaders (Figs. 23F, G, J). In the advanced Podoceridae, uropod 3 is vestigial (Fig. 23L). Within suborder Caprellidea,

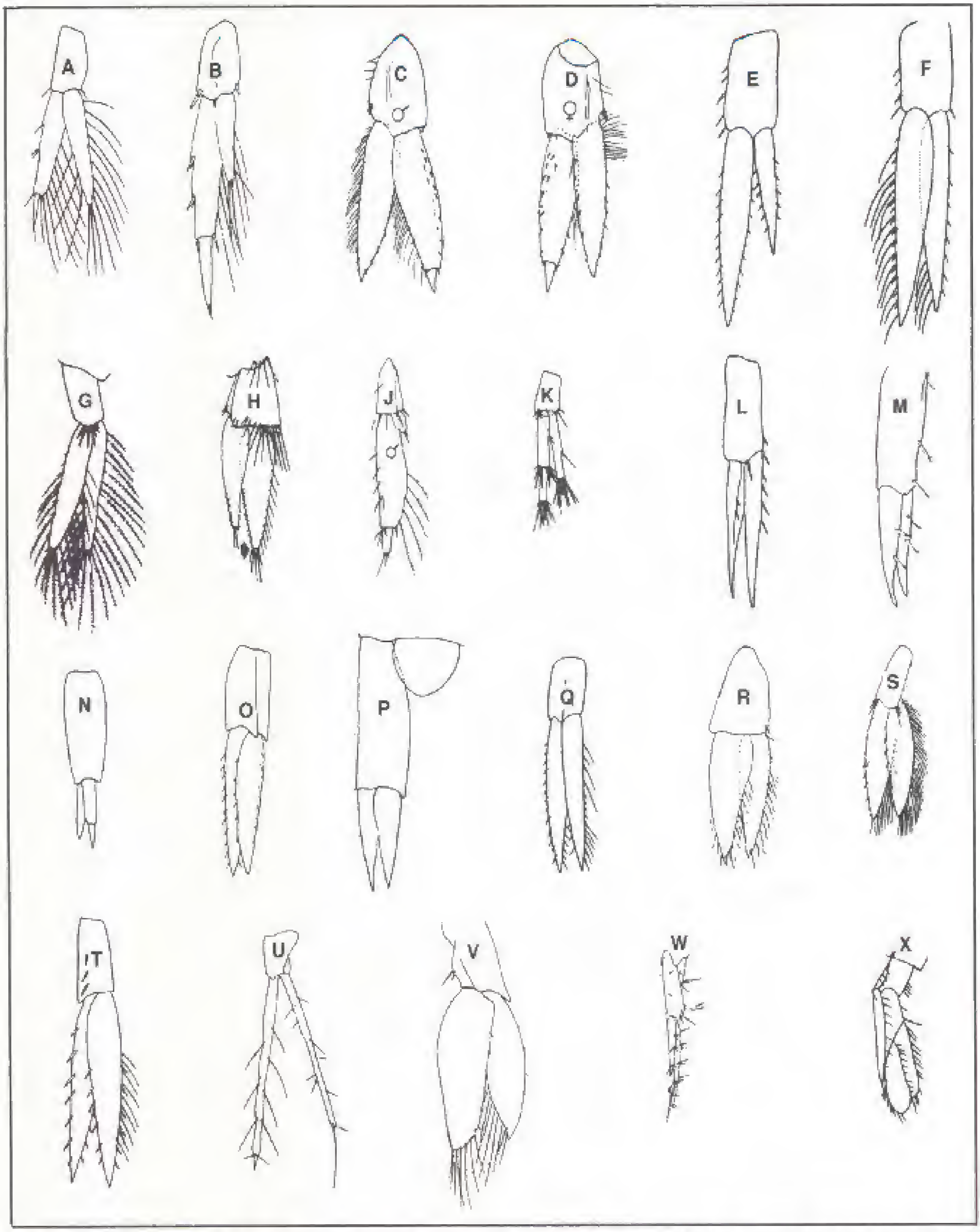


FIG. 21. FORM OF UROPOD 3 IN SUPERFAMILIES OF AMPHIPODA "NATANTIA"
A, B - PHOXOCEPHALOIDEA; C, D - LYSIANASSOIDEA; E, F - EUSIROIDEA; G, H, J - PONTOPOREIOIDEA; K - HAUSTORIOIDEA; L, M - OEDICEROTOIDEA; N, O - STEGOCEPHALOIDEA; P - HYPERIIDEA; Q - SYNOPIOIDEA; R, S - PARDALISCOIDEA T, U - DEXAMINOIDEA; V - AMPELISCOIDEA; W, X - MELPHIDIPPOIDEA. **[after Barnard, 1969, and other sources]**

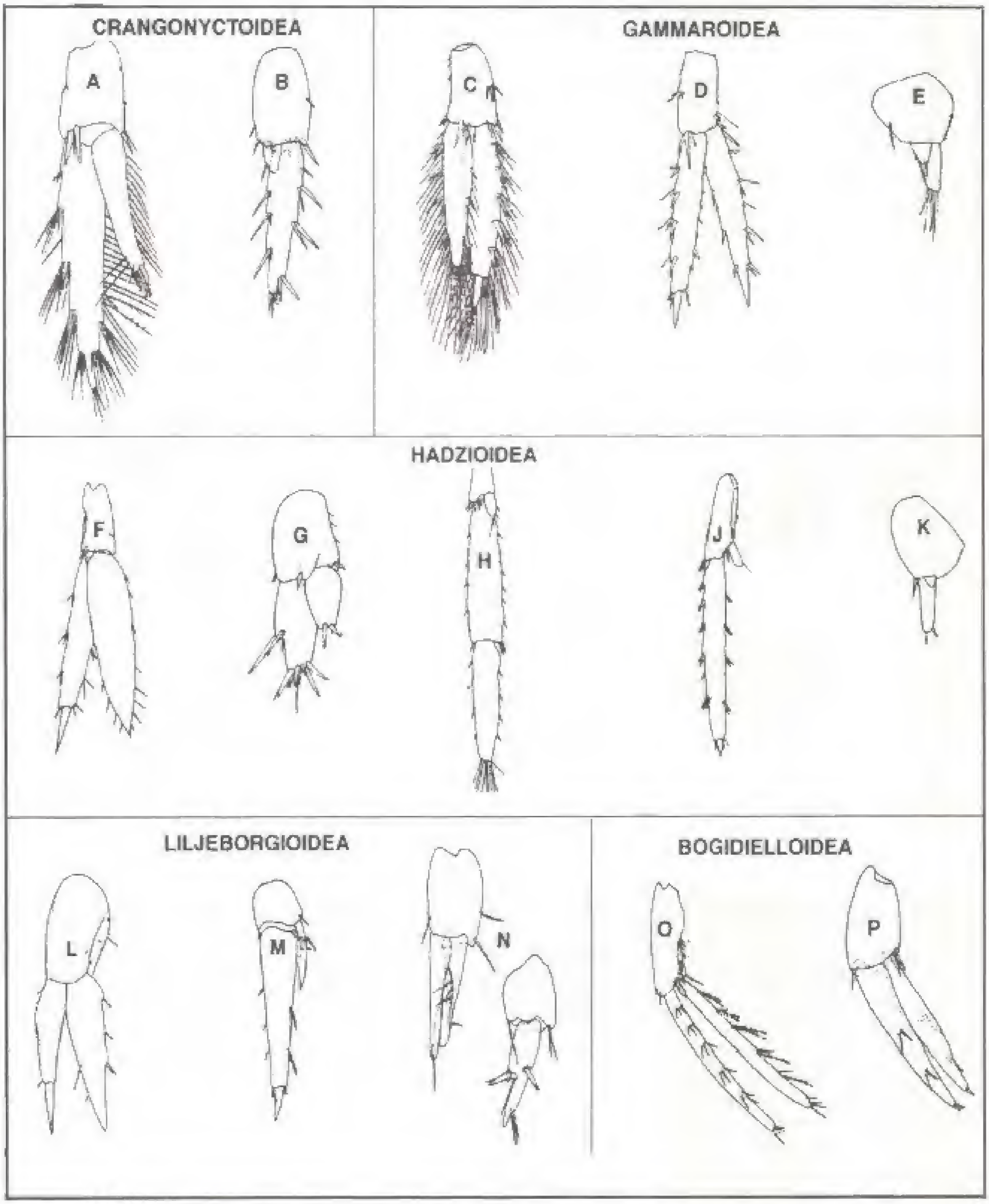


FIG. 22. FORM OF UROPOD 3 IN PRIMITIVE AND INTERMEDIATE AMPHIPODA "REPTANTIA" (from several sources)

A, B - *Austrogammarus, Crangonx* C, D, E - *Gammarus, Mesogammarus, Gammaroporeia*

F, G, H, J, K - *Hadzia, Elasmopus, Eriopisa, Melita, Metacrangonyx*

L, M, N - *Listriella, Salentinella, Pseudingolfiella* O, P - *Bogidiella, Kergueleniola*

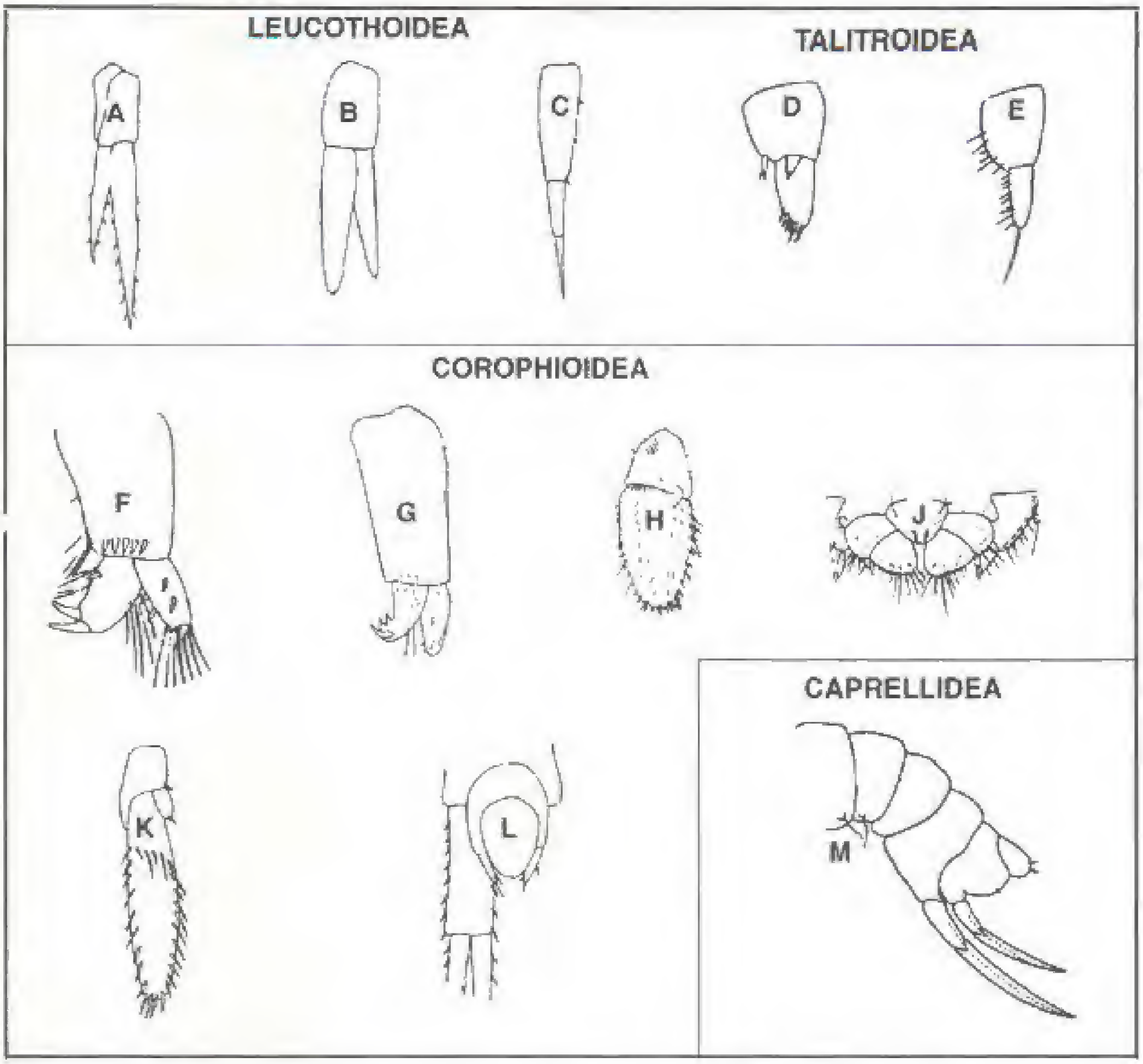


FIG. 23. FORM OF UROPOD 3 IN ADVANCED AMPHIPODA "REPTANTIA"

A - PLEUSTIDAE: B - LAFYSTIIDAE: C - STENOTHOIDAE: D - HYALIDAE: E - TALITRIDAE; F - AMPITHOIDAE G - ISCHYROCERIDAE H - CHELURIDAE J - COROPHIIDAE; K - ICILIIDAE; L - PODOCERIDAE; M - CERCOPIDAE [from several sources]

the abdomen is vestigial in all but the most primitive species, and uropod 3 is entirely lost (Fig. 23M).

In summary, we may note that, with few exceptions, in all amphipod superfamilies in which the reproductive (mating) style is pelagic, uropod 3 (in the male) is of the large natatory, usually aequiramous type, even where the vegetative life style is benthic and/or infaunal. This plesiomorphic form of uropod 3 is diagnostic of the phyletically primitive, gammaridean and hyperiidean superfamily groups, within the Natantia. By contrast, in all superfamily groups that have become secondarily benthic or infaunal, and reproductively benthic or pre-amplexing, the form of uropod 3 is typically of the non-swimming, tactile form. Here the rami are secondarily, and thus apomorphically, reduced or modified in form and function. Only in vegetatively benthic or infaunal forms within the Natantia and within free-living, pre-amplexing superfamilies of Reptantia is uropod 3 found to be strongly sexually dimorphic. Extreme reduction and/or modification of uropod 3 is associated with domicolous, commensal, fossorial, hypogean, or nearly sessile aquatic life styles, or with colonization of supratidal and terrestrial environments. In these forms, the orignal natatory function of the appendage has been lost and/or modified for secondary functions that have presumably enabled the species to penetrate new new environments, new niches and utilize new food resources. Thus, the form of uropod 3 may be utilized as a valuable and useful indicator of phyletic classificatory relationships within the Amphipoda.

PHYLETIC SIGNIFICANCE OF THE FORM OF THE TELSON.

As analyzed previously (Bousfield 1979, 1983, 1986), the deeply bilobate form of the telson is deemed the plesiomorphic condition within amphipodan, peracaridan, and indeed, all malacostracan crustaceans. Conversely, the entire, platelike, or "fleshy" form of the telson is concluded to be the typical apomorphic state, as in Leucothoidean and Corophioidean subfamilies, and represents (typically) a distal fusion of the two primary lobes. A very advanced condition is seen in the Thaumatelsonidae, and many Hyperiidea, where the plate-like telson is fused with the urosome. A less frequent, presumably apomorphic, condition occurs where the lobes become separated throughout their entire length (as in most Gammaroidea and certain Hadzioidea) and attains an extreme separation dorsally on urosome 3 (abominal segment 6) in the advanced fossorial genus *Eohaustorius* (Pontoporeioidea).

A panoramic view of telson types across the spectrum of higher amphipod taxa is provided in Figure **24**. The prototype amphipod is depicted with a bilobate telson, the apex of each lobe having a "notch and spine" configuration. This state may be derived from a pelagic peracaridan (or primitive malacostracan) ancestral outgroup in which the tips of the telson lobes may actually represent vestiges of primordial caudal furcae, as in the phyletic relict Lophogastrida and Euphausiacea. Following evolutionary lines outwards from this base, through each superfamily group, we find that member species and genera having the great-est number of plesiomorphic character states (those nearest the base) also tend to have fully or partially bi-lobate telsons. Conversely, member species and genera with the most apomorphic or derived character states, in balance, usually show the most strongly fused or plate-like form of the telson. The totally bilob-ate apomorphic form may be noted in advanced members of the Gammaroidea and in some members of the Pontoporeioidea (family Haustoriidae).

Derivation of a phyletically "critical" significance to the overall form of the telson is not straightfor-ward, however, because of the obvious independently hooplasious development of the plate-like telson within nearly every superfamily group. Thus, to derive a superfamily group based solely on a plate-like telson would embrace members of at least ten different major groups, and be totally artificial. However, if we look more closely at these evoutionary trends, we may note that within "natant" pelagically mating sup-erfamilies, e.g. Lysianassoidea, Eusiroidea, Pardaliscoidea, Synopioidea, etc., the clearly dominant (typical) form of the telson is deeply bilobate. Conversely, within the more advanced "reptant" superfamilies such as the Leucothoidea, Talitroidea, Bogidielloidea, and Corophioidea, the dominant state is distally notched or plate-like. Perhaps in confirming these general phyletic trends, we may note that the form of the telson in some of the most advanced superfamilies of Natantia (e.g. the Stegocephaloidea, Oedicerotoidea, and the Hyperiidae) is predominantly (or entirely) plate-like. Hyperiids, however, are basically parasitoid, at least for part of their life cycle, and employ salps, medusae, and other pelagic invertebrates as host sub-strata; in this sense they are "reptant" in life style. In the more primitive families within selected superfamilies of Reptantia (e.g. Crangonyctoidea, Gammaroidea, and Liljeborgioidea), retention of the deeply or partly bilobate condition is common.

Undoubtedly, the function of the telson has an important bearing on both its overall, and detailed, form. In pelagic, free-swimming groups, the flexible, bilobate telson may function in balance and in aileron-like stabililization, taking over this function (partly from the antennal squame that is lacking in amphipods (see Watling 1983). In "thruster-swimmers" such as the oedicerotids and hyperiids, the plate-like telson is part of the entire forward-thrusting tail-fan in which the urosomal segments may be fused and strength-ened. Here, the rôle of the telson may be subordinate to that of the larger and presumably more effective component uropods, the rami of which are effectively bilobate and flexible.

On the other hand, within the "reptant", primarily benthic, infaunal, tube-building, commensal, and/or hypogean amphipod superfamilies, hydrodynamic functions of the telson are presumably gradually lost. Other functions such as grooming (see Bowman, 1971), tube-dwelling (see Barnard, 1969; Myers (1988); Conlan (1990), or saltation (as in Talitridae), appear better served by a short plate-like form, with various specialized spinose marginal and apical modifications. A certain degree of sexual dimorphism is retained in the form of the telson, especially within hypogean groups such as the neoniphargid and stygobromid crangonyctoideans, allocrangonyctids, niphargoideans, etc. Here, the telson of the mature male is often relatively elongate and more deeply cleft or notched distally than in the female (vestige of its primordial natatory function?). Unfortunately , detailed and well-documented information on the precise rôle of the telson is lacking for many of the "reptant", as well as more-difficult-to study "natant" groups.

In summary, the present view of evolutionary and phyletic trends in the form of the telson contrasts directly with the views of some others, in which the "fleshy" entire telson was considered plesiomorphic, and led to postulating the Corophiidae as a probable ancestral amphipod type (see Barnard 1969, 1973, Barnard and Karaman, 1980) (Fig. 5) However, the broader more comprehensive studies on the malacostracan telson by Bowman (1974), Schminke (1977), and Schram (1986), while controversial and conflicting, lend little support to the Barnardian view.

At this point we may safely conclude, from an overwhelming array of evidence, that the plesiomorphic or primitive condition of the amphipod telson is bilobate, and that the apomorphic or advanced condition is typically plate-like or apically entire. However, the form of the telson is so frought with life- style modifications at lower taxonomic levels that, per se, it may be phyletically significant only at family, subfamily, or even generic levels, or not at all.

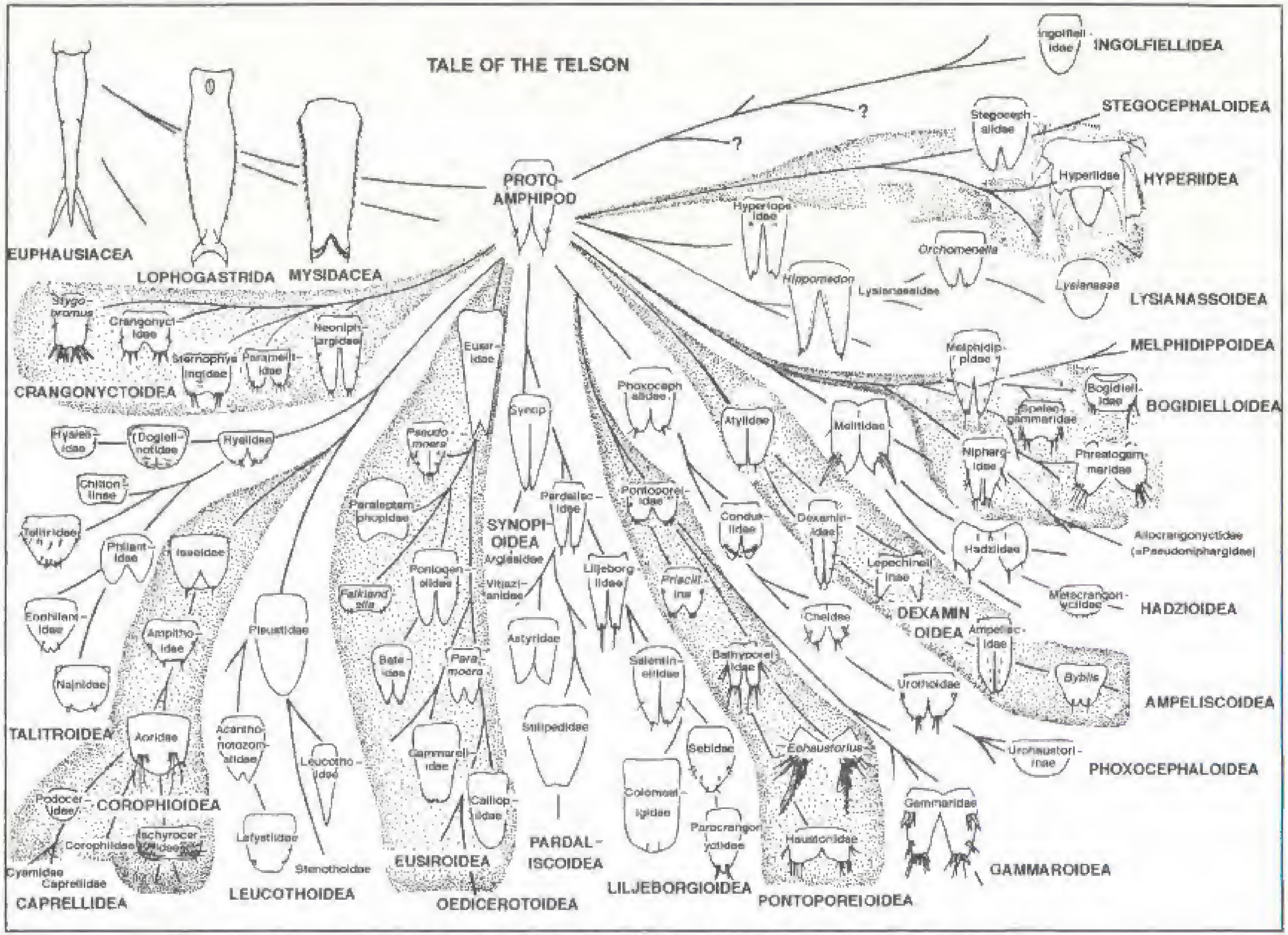


FIG. 24. EVOLUTION OF THE TELSON WITHIN AMPHIPOD SUPERFAMILIES

SPECIAL TAXONOMIC AND PHYLETIC PROBLEMS WITHIN THE AMPHIPODA

The phyletic classification of amphipod crustaceans is rendered especially difficult by the widespread occurrence of character convergence in unrelated taxa of similar life styles, and by the difficulty of selecting suitable outgroup taxa, with or without the use of numerical taxonomic methodology. Assuming natural monophyly of the Amphipoda as an ordinal group within the Malacostraca, an attempt is made here to establish closest phyletic relationships of:
(1) Suborder Hyperiidea
(2) Suborder Ingolfiellidea
(3) Selected hypogean genera of uncertain classification having character states of potential ancestral significance.

(1) Systematics and phylogeny of the Hyperiidea

The Suborder Hyperiidea is divided into two infraorders, 6 superfamilies, and 21 families (Bowman & Gruner, 1973). infraorder Physosomata is generally regarded to be more primitive (showing more plesiomorphic character states) and is thus closer to the presumed ancestral hyperiid than is infraorder Cephalosomata (Bowman & Gruner, 1973). In many respects some members of the Physosomata resemble some non-calceolate callynophorate members of Gammaridea -Natantia, including the broad peraeonal body region, shortened head that often telescopes into peraeon 1, small peraeopod 7, and usual presence of a mandibular palp . The fused urosome segments 1, 2 & 3, the fused inner ramus and peduncles of uropods 1-3, the 1-segmented outer ramus of uropod 3, and plate-like telson are advanced character states that are only occasionally met with (and never totally in combination) in only a few gammarideans (e.g. cyphocarid lysianassids) that tend to have pelagic and neritic life styles that are similar to the hyperiideans.

Sveshnikov & Vinogradov (1987) considered the suborder Hyperiidea toconsist of a heterogenous and apparently polymorphic group of pelagic carnivorous crustaceans. All are hyperiids are pelagobionts; none are benthic. Member species can be grouped into two life form classes of which about 35% are free-swimming predators, and the other 65% exclusively parasites and commensals of gelatinous animals. The former are all members of the advanced Physocephalata whereas the parasitoids encompass all of the Physosomata and several groups within the Cephalosomata. Of the former, the primitive sciniform family members are commensals and strict ectoparasites. These animals have a well developed pleon and urosome, but the grasping adaptations of the appendages are poorly developed or absent. Since the scinid physosomatids are among the most primitive forms of hyperiids, we might reasonably look for ancestral types among the gammaridean amphipods that are similarly free-swimming and weakly parasitoid.

Table II presents a character-state matrix pertinent to physosomatid hyperiids, and to non-calceolate callynophorate superfamilies of Gammaridea-Natantia. The closest (or least different) match (score of 28/40) with the scinid hyperiids is that of superfamily Stegocephaloidea. Similarities with other gammaridean superfamilies (Lysianassoidea and Pardaliscoidea are smaller, in the 40-50% range. These levels are higher, however, than with advanced members of the benthic Reptantia, including the Corophioidea, considered by some to be directly ancestral to the Hyperiidea (see p. 85). Some similarities with stegocephaloideans are conspicuous. Synapomorphies include a telescoped head, an asymmetrically notched upper lip, slightly dissimilar but mainly simple gnathopods, a weakened or shortened maxillipedal palp, shortened peraeopod 7, and nearly plate-like (apically notched) telson. However, stegocephaloideans are much less advanced in retaining an accessory flagellum, deep coxal plates, unfused urosome segment 2 & 3, sometimes 2-segmented outer ramus of uropod 3, and the invariable presence of coxal gill on peraeopod 7, among other plesiomorphic features.

Figure **25** is a resulting phenogram of character state similarities between physosomatid hyperiids and non-calceolate gammaridean Natantia. This phenogram, derived through simple cluster analysis, shows an overall average similarity of hyperiids to callynophorate gammarideans of about 55%. Character state differences that contribute to the relatively low morphological similarity include, in the hyperiids, lack of antennal calceoli and accessory flagellum, absence of a maxillipedal palp,and total fusion of urosome segments 2 & 3, and telson lobes.

Conclusions. These observations suggest that hyperiids may have evolved from a gammaridean ancestral type that was nearest to the present stegocephaloidean body form. Bousfield (1982b) has hypothesized a probable mid-Mesozoic most recent time of origin for callynophorate gammaridean groups, a thesis which, if reasonably correct, would suggest an earlier common ancestry for hyperiid amphipods. The fact that hyperiids exhibit several major differences from closest gammaridean relatives would also suggest that hyperiids have diverged from a common ancestor over a considerable period of geological time. However, despite the remarkable diversity of form , function, and life style shown by members of the Hyperiidea, their derivation from a common ancestor within the much more primitive Gammaridea might justify consideration of their classificatory status as infraordinal within the Gammaridea Natantia. By analogy within the world of vertebrate animals, might the hyperiids be to the gammarideans what the birds are to the dinosaurian euryapsid reptiles?

By similar analysis, members of suborder Caprellidea can be derived from a corophioidean ancestral type (Podoceridae, Laubitz, 1979, 1982) and thus justify reduction of its current subordinal status to infraordinal level.

By contrast, however, the Ingolfiellidea (see also p. 120) possesses unique character states that are more plesiomorphic than anything occurring within the Gammaridea (sens. lat). These include the short unpigmented eye lobes, elongate peduncular segment 3 of antenna 2, partially divided (in-

TABLE I. CHARACTERS AND CHARACTER STATES OF SUBORDER HYPERIIDEA.

CHARACTER	CHARACTER STATE
1. Callynophore (A, male)	1. Present
2. Calceolii (A, male)	2. Absent
3. Accessory flagellum (male, female)	3. Absent
4. Maxilliped palp	4. Usually absent, rarely 1-segmented rudiment
5. Gnathopods 1 & 2 (sexual dimorphism)	5. If present, not significant
6. Brood plates slender (female)	6. No, all broad, bowed margins, smooth
7. Coxal plates 1-4 large	7. If larger, usually significant
8. Pereopod 7 > Pereopod 6	8. Usually smaller to subequal (*Mimonectes* excepted)
9. Coxal gill of pereopod 7	9. Always lacking
10. Pleopods (male) rel to pleopods of female	10. Always more powerful
11. Sexual dimorphism in pereopods	11. Slight, if any
12. Sexual dimorphism of pleopod rami	12. Never
13. Sexual dimorphism of uropods	13. Usually slight (strong in *Lycaeopsis*)
14. Lower lip, inner lobes	14. No, never seen
15. Mandible, left lacinia dentition	15. 8- to 15-dentate
16. Urosome segments	16. Urosomites 2 and 3 fused
17. Telson	17. Entire
18. Upper Lip	18. Notched
19 Maxilla 1, inner plate.	19. Usually not present
20. Uropod 3, outer ramus , segments	20. Always 1-segmented

TABLE II. CHARACTER STATE MATRIX: HYPERIIDEA AND GAMMARIDEAN SUPERFAMILIES

MAJOR TAXON	CHARACTER NUMBER																				P/A IND
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
A. Hyperiidea	0	2	2	2	0	0	1+	1+	0	0	2	0	0	0	1	2	2	2	2	2	21+
B. Stegocephaloidea	0	2	0	0	0	1	0+	2	0	1-	1	0	0	0+	0	0	1	1	1	2	12
C. Lysianassoidea (Hyperiopsidae)	0	1	0	0+	0	2	0	1	0	0	2	0	0	0	1	0	0	0+	0	0	7+
D. Lysianassoidea (Trischizostomatidae)	0	0+	0	0	1	1	1-	2	0	1	0	0	0	0	1	0	0	2	0	1	10
E. Pardaliscoidea	0	2	0+	0	0	0	1	0+	0	1 -	1	0	1	1+	1	0	0	2	0	1	11+
F. Synopioidea	0	2	0	0	0	1	1	0	0	0	0	0	0	1+	0	0	0+	0	0	1	6
G. Dexaminoidea	1	2	1+	1	1	1+	0+	0	1-	0	1	0	1	1	2	0	0	0	0	1	14+
H. Stenothoidea	2	2	2-	0	2	0	0	1	2	1	2	2	0	2	1+	0	2	0	1	2	24
J. Corophioidea	2	2	1	0	2	0	1	0	2	2	2	2	2	2	2	1	2	0+	0	2	27

LEGEND FOR CHARACTER STATES: 0 - PLESIOMORPHIC; 1 - INTERMEDIATE: 2 - APOMORPHIC.

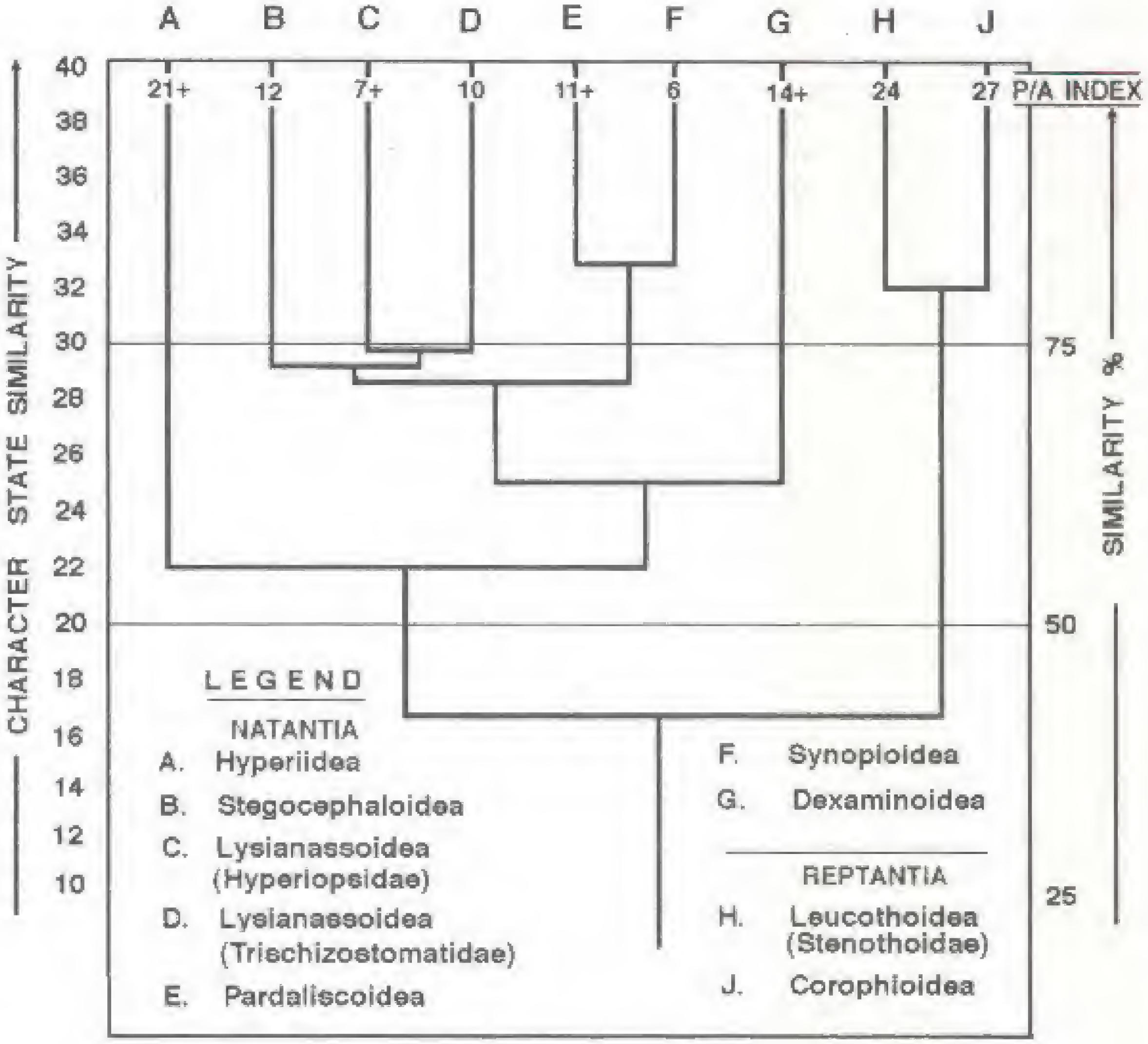


FIG. 25. PHENOGRAM: HYPERIIDEA AND GAMMARIDEAN CALLYNOPHORATE AND NON-CALLYNOPHORATE SUPERFAMILIES

completely fused) segment 1 of the maxillipeds, subsimilar carpochelate gnathopods, and large uropod 2. All of these unique features strongly support continued full subordinal recognition of the Ingolfiellidea.

The distributional-ecological occurrence of the Ingolfiellidea, world-wide in marine and hypogean in continental freshwater, supports not only their classificatory distinctiveness but their probable great antiquity (late Paleozoic, per Bousfield & Conlan, 1990)

Distributional-Ecology of hyperiid amphipods

Both hyperiids and stegocephaloideans are exclusively marine, in fully saline (> 30‰) waters, well away from the immediate influence of land run-off. Both groups are present over the shelf and slope, and in the abyss, or exhibit vertical diurnal migrations from below the euphotic zone. Stegocephaloideans are mainly epibenthic, but *Parandania boeck* is mesopelagic (Moore & Rainbow, 1989), and lives in association with medusae (e.g. *Atolla parva*). Also stegocephaloideans are found mainly in cold-water regions, as are the more primitive members of the Hyperiidea, the Physosomata, and some of the more primitive members of the Cephalosomata (of family Hyperiidae).

As noted above, at some stage in their life history, most hyperiids are parasitoid, usually in relationship with the Coelenterata, Tunicata, and other jelly-like pelagic animals. Stegocephaloid-eans are symbiotic with sponges, tunicates, sessile coelenterates, and other cnidarians (Moore and Rainbow, 1984, 1989). Such associations indicate lengthy evolutionary development, and classificatory stability, further underscoring the suitability of stegocephaloideans as a phyletic outgroup taxon for the Hyperiidea.

The Haustorioidea Problem

The phyletic classification of fossorial, free-burrowing amphipods having a the so-called "haustoriid" facies has long posed a particulary difficult problem for systematists. The "haustoriid" superfamily concept variously encompasses families of *Haustorius*-like animals and pontoporeids of northern coastal waters, and urothoids, urohaustoriids, phoxocephalids, phoxocephalopsids, platyischnopids, zobrachoids, cheids, condukiids, plus a few other enigmatic genera of mainly austral marine regions. Differing views on the taxonomic boundaries of family and superfamily diagnoses, and on the phyletic importance of certain "fossorial" character states, have resulted in two principal recent phyletic classifications. In essence, the concept of the Haustorioidea proposed by the late J. L. Barnard broadly encompasses all of those groups (Barnard & Drummond, 1982; Barnard & Karaman, 1991). A further concept, proposed by one of us, restricts the Haustorioidea to the northern families Haustoriidae, Pontoporeiidae, and Bathyporeiidae, and relegates the austral families to the superfamily Phoxocephaloidea (Bousfield, 1979a, 1982, 1983). Since component groups encompass most of the littoral marine sand-burrowing amphipods of the world, form an important element of marine food energy cycles, and are proving to be useful indicators of sedimentary environmental quality, problems concerning their natural classification merit our further systematic attention.

An assessment of phyletic relationships of haustoriid amphipods was undertaken and presented relatively recently by one of us, but the results remain formally unpublished (Bousfield, 1989). Characters found to be of important phyletic significance included general body form, size and shape of the rostrum, presence of antennal sensory organelles, structure and "dactylation" of the posterior peraeopods and maxillipedal palp, form of the pleopods, type of mouthparts, and differences in character states of the telson, uropods, and other appendages. The major difficulty in sorting out the phylogeny of fossorial animals is the "look-alike" problem, i.e. the high incidence of convergent evolution within nearly every character and character state, of all the family groups investigated. However, close and careful examination of these character states, in relationship to those that tend to be relatively independent of fossorial life style (e.g. significant in reproduction, feeding, and swimming), in combination, provides a more reliable basis for sorting out homoplasious similarities from true phyletic similarities. On this methodological premise, evidence from the evolutionary direction, or trending, within pertinent character states suggested a basic phyletic difference between the two major groups. Thus, the northern haustoriids appeared to be more closely related to gammaroidean amphipods, and of relatively recent origin, perhaps associated with the opening of the Atlantic Ocean during the Mesozoic Era. The southern group was found phyletically more primitive and isolated from other major taxa, and of greater antiquity, originating probably prior to the Gondwanian continental breakup.

In this brief recapitulations of the 1989 analysis, we here consider in detail one main character state, the form of the rostrum (Fig. 26). The upper row shows a dorsal outline of the head, rostrum and proximal peduncular segments of representative species of fossorial pontogammarids within the Gammaroidea (A), and of a bathyporeiid and two haustoriids within the Pontoporeioidea (B, C, D). The middle row gives similar views of representative species within urothoid(E), urohaustoriid(F), phoxocephalopsid(G), and zobrachoid(H) family complexes, within urothoid type phoxocephaloideans The bottom row gives similar views of species within subfemilies of Phoxocephalidae (H, J, K), Cheidae (L), and Platyischnopidae (M). Trends and key differences in the form of the rostrum are pronounced. Thus in the "hooded heads" (Phoxocephalidae) and "shark-snouts" (cheids and platyischnopiods)(bottom row) the rostrum is variously elongate and extends much beyond the lateral head lobes. In the urothoid type animals (middle row), the rostrum is short but extends distinctly beyond the lateral head lobes. In the gammarids, pontoporeiids, and haustoriids (top row), however, the rostrum is vestigial or very short, and extends little or not beyond the lateral head lobes. In these latter groups, the substrate-penetrating function performed by the prow-like rostrum of the phoxocephalids and urothoids is apparently performed by the distally narrowing and closely approximated peduncular segments of the first antennal pair.

Other major character states have been correlated with differences in form of the rostrum (Bousfield, 1989). Thus, family members of the upper row all possess strongly deflexed urosomes ("bent backs"), weakly dactylate (or adactylate) peraeopods and maxilliped palp, variously dissimilar and weakly sexually dimorphic gnathopods 1 & 2, unreduced (gammaroidean) mouthparts, pleopods reproductively non sexually dimorphic, broad to medium broad brood plates, and advanced, gammaroidean-type antennal calceoli (when present), among other differences. Family members of the middle and lower rows, all possess weakly deflexed urosomes ("straight backs"), strongly dactylate peraeopods and maxilliped palp, subsimilar and non sexually dimorphic gnathopods 1 & 2, strongly reduced or modified (carnivorous) mouthparts, high incidences of reproduct9ively sexually dimorphic pleopods, linear or sublinear brood plates, and primitive crangonyctoidean-type calceoli (when present).

In all these instances, these differences are here considered of major phyletic significance rather than of convergent similarity. Accordingly, members of the family Haustoriidae are included here with the phyletically related Pontoporeiidae and Bathyporeiidae, within superfamily Pontoporeioidea, and allied with superfamily Gammaroidea of the northern hemisphere (Fig. 30, Table III). Members of the southern fossorial family groups are here maintained within superfamily Phoxocephaloidea,that is phyletically isolated from other marine superfamily groups, but exhibits character states that perhaps indicate distint relationships to the Crangonyctoidea, now restricted to continental freshwaters of the world.

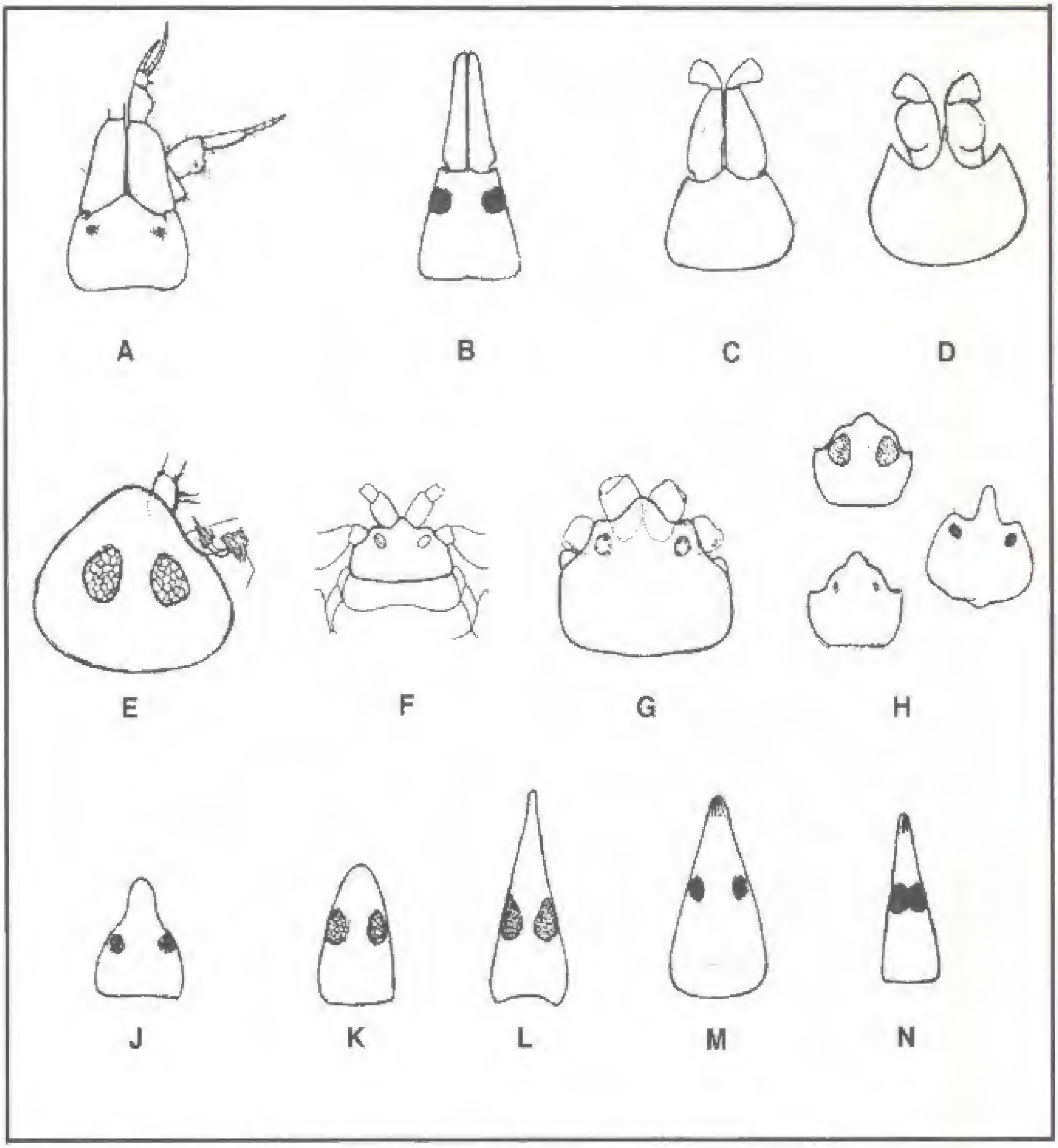


FIG. 26. SIGNIFICANCE OF ROSTRUM IN SUPERFAMILY RELATIONSHIPS

TOP ROW	A Pontogammaridae B Bathyporeiidae C Haustoriidae *(Protohaustorius)* D Haustoriidae (*Haustorius*)
MIDDLE ROW	E Urothoinae F Urohaustoriinae G Phoxocephalopsinae H Zobrachoinae
BOTTOM ROW	Phoxocephalidae: J Tipimeginae K Brolginae L Phoxocephalinae M Cheidae N Platyischnopidae

The Classification and Phyletic Position of the Ingolfiellidea.

As noted by Schram (1986), the classification of the Ingolfiellidea has been the subject of modest controversy. Following discovery of the first species of *Ingolfiella* by Hansen (1903), the animals were first classified as a new family within the Gammaridea (e.g. Stebbing, 1906). Following Reibisch (1927), and discovery of further new freshwater and marine species, the group was elevated to separate subordinal status within the Amphipoda, a classification now accepted by most workers. However, Bowman and Abele (1982) and Bowman (pers. communic., 1992) would relegate the group to family level status within the Gammaridea. Here, we briefly re-examine its major character states and re-evaluate their significance in phyletic classification (see also pp. 125-26).

Suborder Ingolfiellida encompasses a small group of blind, vermiform, hypogean and fossorial amphipods occurring nearly world-wide in both marine and freshwater habits (Bousfield, 1982a; Stock, 1977). They occur over a remarkable range of hypogean and infaunal habitats, and are the only freshwater amphipods presently known from fresh waters of south-central Africa, north of Zimbabwe. About 40 species have been described to date. They are classified in several genera and subgenera belonging to two families, the Ingolfiellidae Hansen, 1903 and the Metaingolfillidae Ruffo, 1969. The latter family is monotypic and in some features more primitive than members of the speciose family Ingolfiellidae. The former is here considered likely to reveal ancestral character states that might link the suborder with other amphipod types and with other peracaridan taxa.

Some of the principal morphological features of *Metaingolfiella mirabilis* Ruffo, 1969, are shown in Fig. 27. Descriptive details can be found in Ruffo's original work (loc cit.) and in family-level compendia by Bousfield (1982a) and others. This large species exhibits the following morphological features mostly previously considered to be of major taxonomic and phyletic significance:

1. Antenna shorter than antenna 2, with accessory flagellum
2. Antenna 2, peduncular segment 3 elongate , >1/2 length of segment 4
3. Antenna 2, segment 1 free, not concealed by lateral head margin
4. Unpigmented ocular lobes present, at the lateral anterior head process.
5. Paired maxillipeds with distally separated (unfused) basal segments
6. Gnathopods large, dissimilar, raptorial, strongly carpocheliform (carpus with palm, against which closes the combined propod and dactyl), not sexually dimorphic.
7. Peraeopods 3-7, dactyls very short.
8. Pleopods biramous, rami annulate, pleopod 1 complexly sexually dimorphic.
9. Uropod 2 much larger and longer than uropod 1, almost pleopod-like
10. Telson lobes fused to a narrow plate, with paired distal penicillate setae

Character states 2, 3, 4 , 5, 6, 8, and 9 are all considered plesiomorphic and found nowhere else within the Amphipoda, let alone in hypogean families and superfamilies within suborder Gammaridea. This taxon is therefore morphologically unique within the Amphipoda, cannot be classified within suborder Gammaridea, as presently conceptualized, and therefore merits full subordinal status of it own.

It is difficult to extrapolate character states of a highly modified vermiform amphipod to a form in which these characters might have existed in the presumed epigean ancestors of the Ingolfiellidea. Homoplasious reduction of locomotory appendages and mouthparts, and loss of pronounced sexual dimorphism, is almost the rule in fully hypogean amphipods. As noted in the hypothetical phyletic tree of the Amphipoda (Fig. 30, p. 126), the ancestral epigean ingolfiellid was almost certainly callynophorate, with primitively calceolate antenna, much as in modern crangonyctoideans, and with a terminal male stage. The eye lobes may have borne pigmented stalked eyes, and peduncular segment 3 of antenna 2 a vestigial squame. The gnathopods were almost certainly non sexually dimorphic and non preamplexing. However, as noted previously, character nos. 2, 3, 4, 5 and 8 occur, in more conspicuous form, within some extant petalophthalmid Mysidacea but, to date, nowhere else within potential ancestral outgroup peracaridans.

As noted above, the Ingolfiellidea occur widely in both fresh and salt water, from the shore line to the abyss, nearly world wide. On the other hand, both the Hyperiidea and the Caprellidea are strictly marine and of restricted ecology and life style. Ingolfiellids overlap distributionally and ecologically with many other hyopogean amphipod groups, especially with bogidieloideans and niphargids but are readily distinguishable. Whereas the ingolfiellids possess several symplesiomorphies but no synapomorphies vis-a-vis the Gammaridea, the reverse is true of the Hyperiidea and Caprellidea. We therefore conclude that the case for continued recognition of the Ingolfielliea at subordinal level is strong whereas that for the Hyperiidea and Caprellidea merits further consideration.

Phyletic Relationships of Large Hypogean Amphipods

As in the fossorial amphipods, the phyletic placement of hypogean amphipods is subject to problems of convergent evolution because of the specialized but relatively uniform nature of the phreatic environment. However, such problems tend to be evidenced in rather different and mainly non reproductively related aspects of their systematics. Holsinger (1993) has comprehensively reviewed the distribution of the world fauna of 740 hypogean amphipod species that are distributed among 36 families and 12 superfamilies or equivalent groups. Most of these occur in the northern hemisphere, but diversity is relatively high among groundwater amphipods

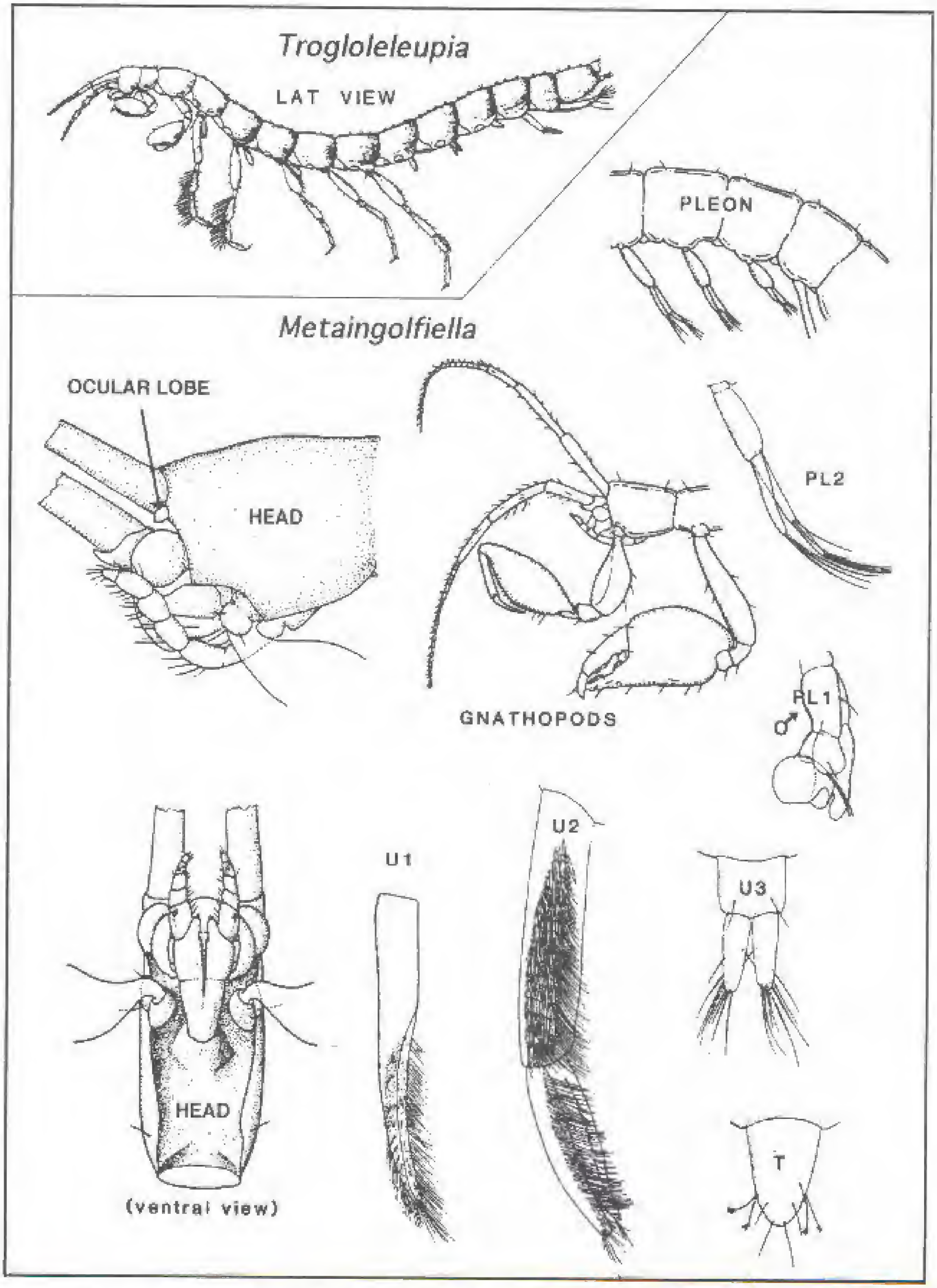


FIG. 27 MORPHOLOGICAL FEATURES OF INGOLFIELLIDEA (mainly after Ruffo, 1969)

of the southern continents. Most species are readily assignable to family and superfamily categories, but some taxa remain enigmatic and difficult of satisfactory phyletic placement.

In 1986, Notenboom described a relatively large, carnivorous amphipod species from wells and a cave lake near Valencia in eastern Spain. The animal appears basically gammaroidean in general features, but is remarkable in possessing calceoli on both antenna of both sexes. As noted in fig. 11, this is a strongly plesiomorphic feature that is found only among the relatively primitive superfamily groups and within very few other epigean gammaroidean subgroups (e.g. *Paramesogammarus*). The species was fully figured and described by Notenboom and is refigured here for comparison with possible closely related ingroups (Fig.28).

Sensonator valentiensis appears more gammaroidean than any other superfamily group, especially in character states of the antennae, some mouthparts (e.g. simple lower lip), anterolobate coxae, dorsal abdominal spination, uropod 3, telson, and surface ultrastructure. However, males are smaller than females, the gnathopods are non sexually dimorphic, and some mouthparts, especially the mandible, are rather strongly modified for an apparently specialized feeding role. After comparing the species with member of the Liljeborgiidae, Pardaliscidae, Niphargidae, Crangonyctidae, Bogidiellidae, *Pseudoniphargus*, and other hypogean groups, Notenboom was unable to place the animal phyletically. However, he refrained for formally proposing a new family or higher level taxon for its reception, and hence has left the matter open for further consideration.

As seen in our Fig. 28 the differences between *Sensonator* and other major regional groups of hypogean amphipods such as niphargids, typhlogammarids, and bogidiellids are fairly obvious and need not be detailed here. However, if general features of the species are compared with regional littoral marine species within the Melphidippoidea, some strikingly similar character states may be noted. Thus, North Atlantic species of *Cheirocratus* and *Casco* have similarly sharply incised inferior head sinuses, antenna 1 much shorter than 2, anterior coxae diminishing in size posteriorly, gnathopods unequal in size (2 the larger), peraeopods 5-7 long and nearly homopodous, with short dactyls and tendency to strong distal setation, strongly aequiramous uropod 3, and telson short and bilobate. These species also have narrow brood plates and lack a coxal gill on peraeopod 7.

We concur with Notenboom's evolutionary scenario in which a frees-swimming marine ancestor probably invaded macroporous biotopes in the littoral karst. We would suggest that as far back as the Cretaceous, ancestral melphiddipoideans may have been calceolate and much more numerous than their present relict status might indicate. Such ancestral types may once have occupied littoral biotopes now taken over by the more advanced hadzioideans (melitids). In our view, modern melphidippoideans merit further study as an extant relict group that may well have sprung from the same common ancestor as *Sensonator*.

A somewhat similar problem of phyletic classification has concerned *Phreatogammarus fragilis* described by Chilton more than 100 years ago from stream beds in the South Island of New Zealand. He assigned the species to family Gammaridae were it remained following its redescription and the addition of further species by Hurley (1954). The species is refigured here, for comparison with other regional epigean species and with other hypogean world genera of possible phyletic relationships (Fig. 29).

The animals superficially resemble some gammaroideans of the northern hemisphere, including species of *Typhlogammarus* (Fig.28).Characters of strongest similarity are found in the elongate antennae, with strong accessory flagellum, large, sexually dimorphic gnathopods (2 the larger), elongate peraeopods with antero-lobate coxae, dorsally spinose urosome, and large brood plates. However, differences may be noted in the mouthparts, peraeopod dactyls, uropods, telson, and a form of sternal gill is present, all of which precludes direct assignment within any known modern group of gammaroideans. Although *Phreatogammarus fragilis* in continental in New Zealand, it bears a superficial resemblance to medium and large hypogean species such as *Pintaweckelia grandis* Stock from wells in the Caribbean continental island of Haiti, and to *Carnarimelita janstocki* Bousfield from anchialine cave pools in the volcanic Hawaiian Islands (Fig.29. Although *Phreatogammarus* is readily distinguishable from these two forms, especially in the mouthparts, coxal gills and uropods, these two forms appear at least remotely phyletically related and merit further investigation in this regard.

By fortunate chance, one of us (ELB) was able to collect material of additional epigean estuarine and freshwater species, here designated as *Phreatogammarus* sp. 1 and *Phreatogammarus* sp. 2 respectively (Fig. 29). A preliminary report on this material was presented at the International Crustacean Symposium in Sydney, in 1980, but the new taxa have not yet been formally described. These species are similar to the phreatic species, except for their smaller size, pigmented eyes, and more strongly sexually dimorphic gnathopods. They form a taxonomic and ecological series, from marine and estuarine, through fluvial epigean to fluvial hypogean biotopes. We might reseasonably conjecture, therefore, that this series reveals a direct pathway of egress by which littoral marine organisms have penetrated hypogean fresh waters in the past, not only in austral regions, but world-wide.

Except for the relatively short telson lobes, the estuarine species also demonstrates a remarkable overall similarity to species of *Hornellia*, a tropical and Indo-Pacific genus within superfamily Melphidippoidea. The genus *Phreatogammarus* may well have shared a common ancestor with present-day littoral marine melphidippoideans. Thus, pending more detailed comparison over a broader spectrum of material, the two groups are placed tentatively on the same major evolutionary branch of the revised and updated amphipod phyletic tree (Fig. 30).

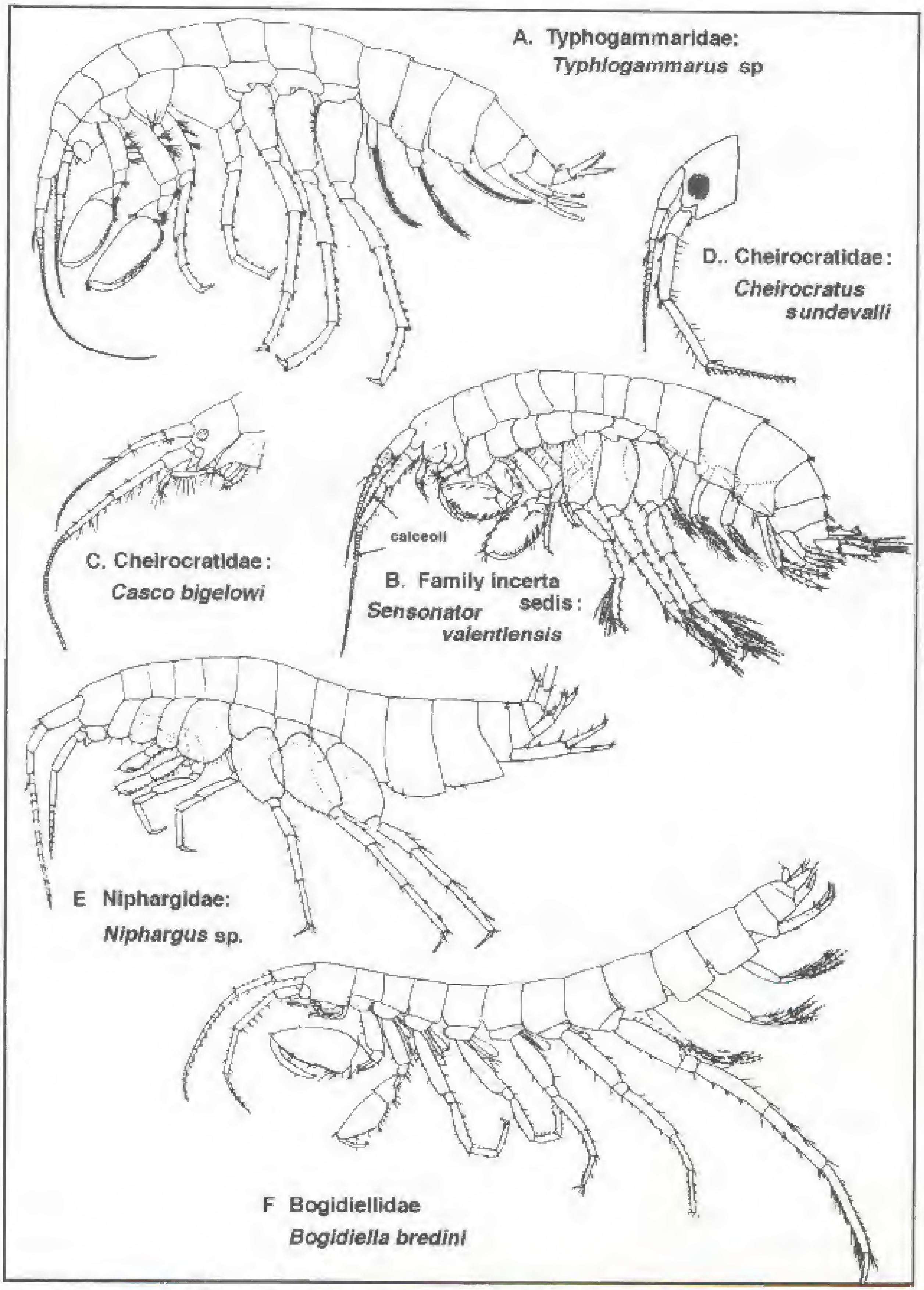


FIG. 28 CONVERGENT MORPHOLOGIES IN LARGE HYPOGEAN AMPHIPODS [from Notenboom (1986) and various sources]

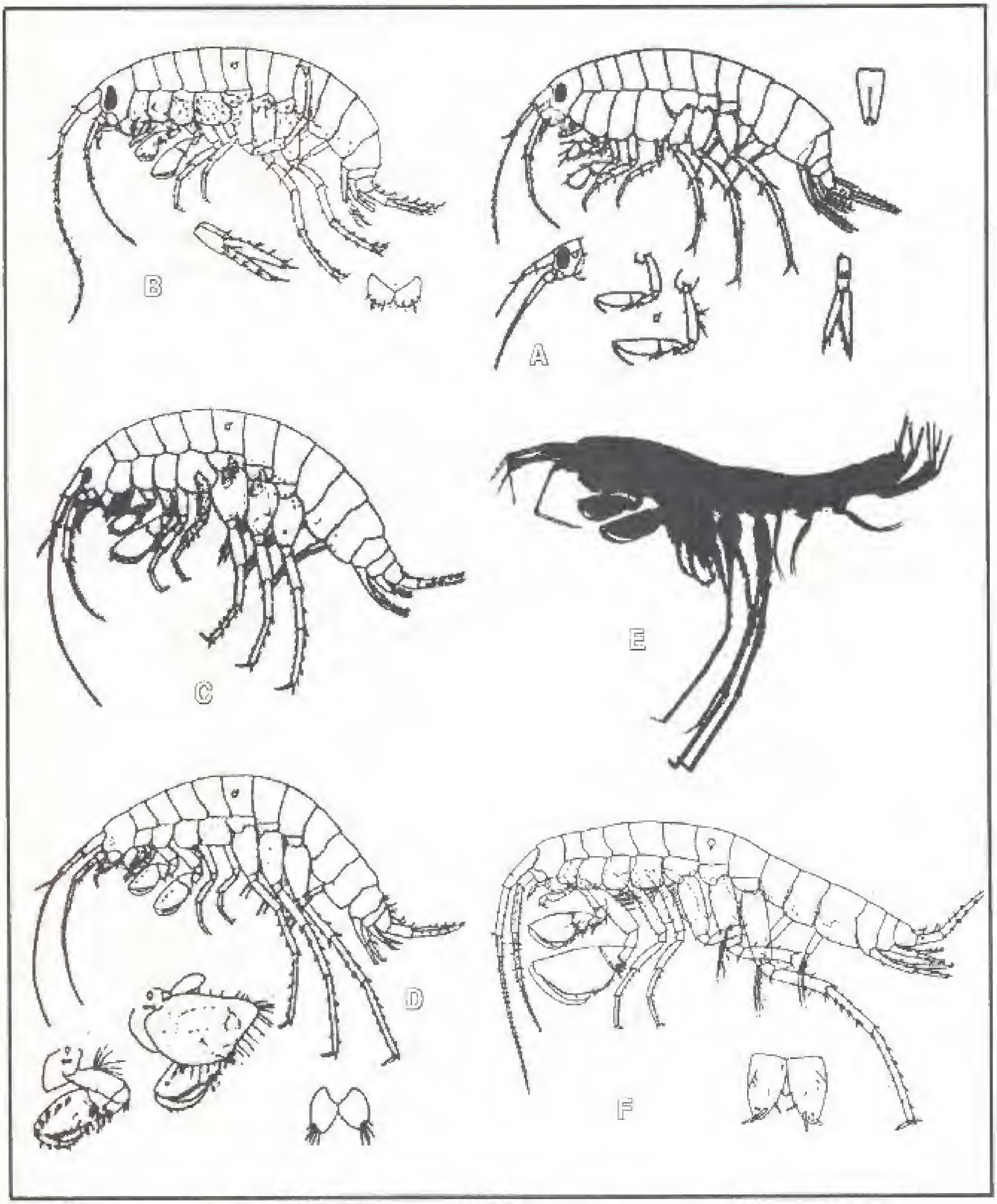


FIG. 29 PHREATOGAMMARUS SPP. AND SELECTED MELPHIDIPPOIDEA AND HADZIOIDEA
A. *Hornellia sp.* B. *Phreatogammarus sp. 1* C. *Phreatogammarus sp. 2* D. *Phreatogammarus fragilis Chilton* E. *Pintaweckelia grandis Stock* F. *Carnarimelita stocki Bousfield*

Phylogenetic tree.

Long before the advent of numerical taxonomic analysis, hypothetical phylogenetic relationships between higher categories of classification of organisms had classically been presented in a branching tree-like arrangement. In a morphological treatment, the plesiomorphic character states are most strongly evinced in taxa, extant or extinct, that are closest to the trunk and main branches, and the apomorphic or advanced and specialized features are best developed in taxa placed near the branching extremities. In effect, the phylogenetic "tree" may be viewed as a form of cladogram in which the character states are ordered and arranged "parsimoniously", but without numerical basis. Brusca & Wilson (1991) have employed cladistic methodology in phylogentic analysis of the Isopoda, resulting in major classificatory recommendations for the 10 suborders within this very diverse, primarily benthic, and relatively ancient group of peracaridans. However, the universality applicability and adequacy of cladistic analyses for this purpose has been questioned by some (e.g. Gosliner & Ghiseln, 1984). A full cladistic analysis of the Amphipoda is beyond the scope of this paper. Serious problems concerning character state homoplasy, and the status of so-called "intermediate" taxa have yet to be resolved. However, a phyletic tree based on "first principles" is here provided as a useful visual basis for eventual numerical establishment of a true phyletic classification of the Amphipoda.

In this respect, Bousfield (1979a) has proposed a tree-like arrangement for amphipod suborders and superfamilies that is here refined and updated on the basis of new information and expanded analysis of major characters and character states (see Fig. 30). The thickness of the branches was roughly proportional to the number of extant species in each subtended major category. In the early version, the "stem" taxa lay within a boundary or envelope of those possessing a pelagic reproductive and terminal male stage. Envelopes of selected plesiomorphic character states such as the presence of postero-lobate coxae of peraeopods 5-7, and calceolate antennae also encompassed superfamilies, closer to the tips of the branches, in which mature males were benthic, preamplexing, and of indeterminate life stage.

The present version of the tree (Fig. 30) is essentially similar. During the past 15 years the number of species in each group has increased, variously, by only about 5-10%, few major new taxa have been discovered, and the ordering of character states has remained basically unchanged. However, the callynophore (Lowry, 1986), calceoli (Lincoln and Hurley, 1981), brush setae, and other sensory and swimming structures of reproductive males (p. 88) have since been developed as significant indicators of phyletic relationships. Emphasis on such parameters has here altered the position of the main trunk which now centrally subtends superfamilies of Natantia leading to the most highly advanced and modified Hyperiidea. These taxa are marked by the plesiomorphics of Table I (p.) that include, in the male, a more slender and flexible urosome, powerfully natatory pleopods, and well-developed, usually plumose-setose uropod 3 and tail fan. Calceolate antennae are restricted to the more primitive members of Natantia and to more advanced subfamilies that have variously penetrated lotic-water environments of coastal estuaries and freshwaters (e.g. some pontogeneiids and calliopiids within Eusiroidea; paracalliopiids and exoedicerotids within Oedicerotoidea). The Lysianassoidea is the only group within Natantia to retain callynophore, calceoli, and brush setae, thus remaining closest to the presumed gammaridean ancestral type, and confirming the classical ancestral position set forth by Sars (1895) and Stebbing (1906). The pelagic males of nestling and tube-building Dexaminoidea and Ampeliscoidea have virtually lost the callynophore, but retain antennal brush setae, powerful tail fan, and bilobate telson. In this respect, the Melphidippoidea are similar, but in their development of weakly sexually dimorphic gnathopods, appear transitional to members of the Reptantia. The monotypic genus *Sensonator* (of Notenboom, 1986) is here proposed (p.) as a primitive early offshoot that still retains antennal calceoli of the presumed marine ancestral melphidippoidean. Primitive members of the fossorial Pontoporeioidea (excluding Haustoriidae) and the Phoxocephaloidea (most) have totally lost the antennal callynophore but have retained brush setae and calceoli. As noted previously, natant superfamilies with calceoli are primarily cold-temperate and arctic in distribution, those without are primarily tropical and warm-temperate. The coxal gill of peraeopod 7 is retained widely within the Natantia, and is plesiomorphically pleated or dendritic in pelagic males of Lysianassoidea, Eusiroidea, Dexaminoidea, and Ampeliscoidea.

The superfamilies of Reptantia are placed nearer to the branch tips. Those on the right side of the tree tend to possess more plesiomorphic character states such as homo-podous peraeopods 5-7, with postero-lobate coxae, and generally lack an ecdesial (baso-facial) spine on uropod 1. Among fresh-water members, the occurrence of various types of sternal gills is widespread (e.g. most crangonyctids, hyalellin talitroideans, pontogeneiid eusirids and *Falklandella*, and paracrangonyctid liljeborgiids). Categories of Reptantia on the left side of the tree are advanced in those same character states and, in fresh water members (e.g. of Gammaroidea, Hadzioidea, Bogidielloidea), sternal gills are lacking or very rare. The coxal gill of peraeopod 7 is retained only in the most primitive members of Reptantia (e.g. most Gammaroidea and Crangonyctoidea) and that of peraeopod 2 is lost in many corophioideans and all caprellidans.

On the left side of the tree, the primitive hypogean and fossorial Ingolfiellidea (p. 126) diverged early from the many evolutionary trunk. Its presumed epigean free-living ancestors were almost certainly callynophorate and calceolate but little except some mysid-like character states can be deduced from comparative morphology (p. 80) and no trace remains in the very limited amphipod fossil record. The hadzioidean and corophiodean superfamilies underwent progressive reduction of antennal sensory structures, diminu-

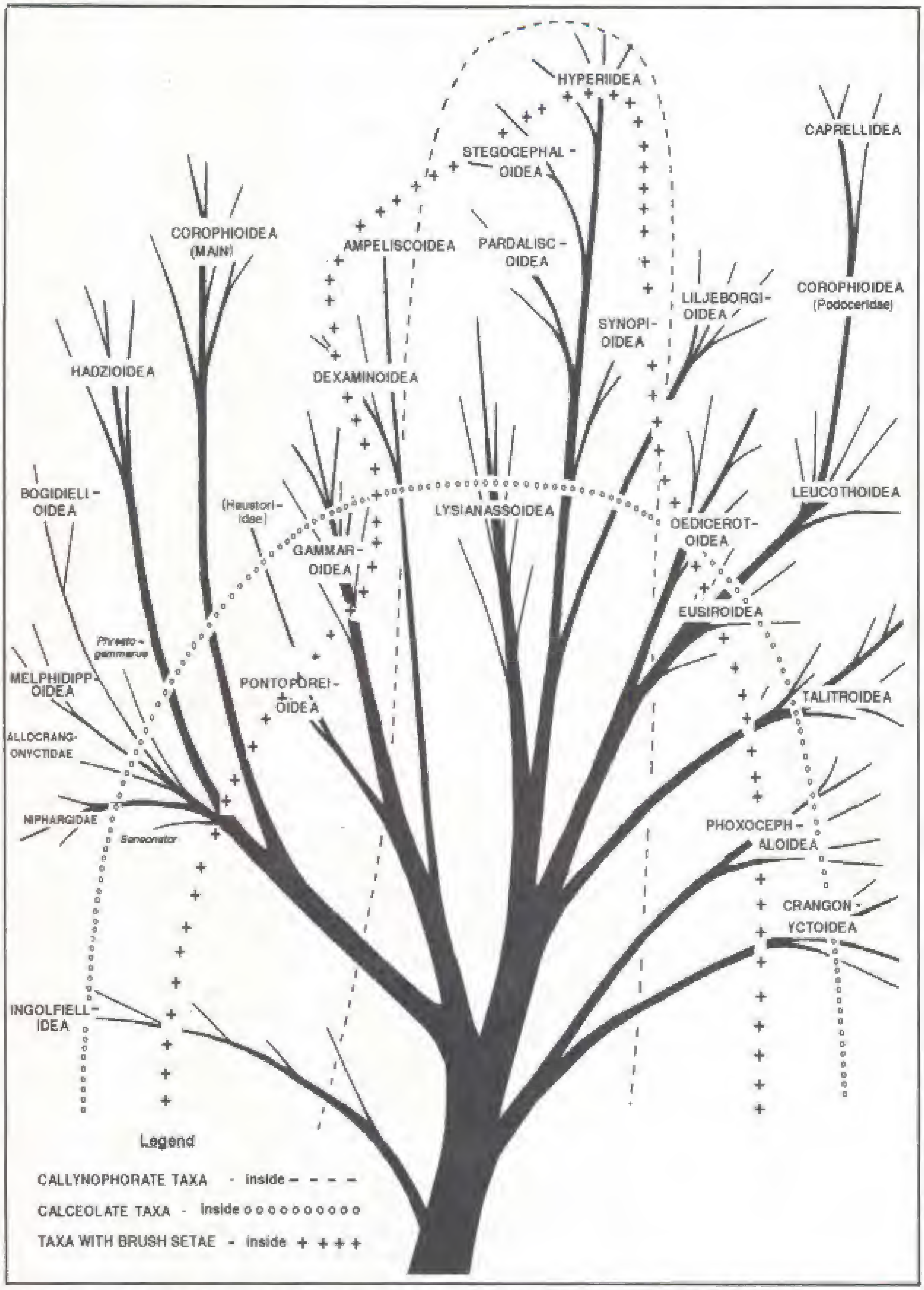


FIG. 30. REVISED PHYLOGENETIC TREE OF AMPHIPOD SUPERFAMILY RELATIONSHIPS

tion of pleopods, uropod 3 and tail fan, and fusion of telson lobes, but enormous development of pre-amplexing and mate-guarding gnathopds in the male (p. 105), apparently associated with benthic and domicolous life styles. The relatively primitive, mainly freshwater gammaroideans have lost callynophore and brush setae, but many have retain antennal calceoli, and fairly strong development of uropod 3, tail fan, and bilobate telson. Gnathopods of the male function in pre-amplexus, rather than in agonistic mate-guarding. Presumably related to the natantian melphidippoideans are the allocrangonyctids and pseudoniphargids, on the one hand, and the phreatogammarids and bogidielloideans on the other (p.126).

On the right side of the tree, the crangonyctoideans are clearly reptant, having lost the callynophore and brush setae, undergone strong reduction of pleopods, uropod 3, and fusion of telson lobes, and are predominantly hypogean in life style. The Crangonyctoidea ranks as the most primitive of reptant superfamilies in which males are typically smaller than females, with non-preamplexing gnathopods, and terminal in life stage.. Their widespread retention of calceoli, of a very plesiomorphic form, provides a plaus-ible link with the marine Phoxocephaloidea. Indeed, *Perthia* (the most primitive crangonyctoidean) possesses a natatory uropod 3, strongly bilobate telson, primitively calceolate antenna 1 (male only), specialized carnivorous mouthparts, squarish coxal plates, sexually non-dimorphic raptorial gnathopods, and elongate peraeopod 6, features that are reminiscent of many Australian Phoxocephalidae (see also Williams & Barnard, 1988). In association with their freshwater and terrestrial evolutionary thrust, and ability to saltate in air, the talitroideans have undergone very marked reduction of the antennae and sensory structures, of pleopod and uropod 3, and fusion of telson, and powerful development of agonistic and/or pre-amplexing gnathopods, but have otherwise remained generalized and primitive in general body form. Marine members of the Liljeborgioidea (e.g. of Liljeborgiidae, Sebidae, Colomastigidae) are variously specialized for commensal life style, with strongly sexually dimorphic gnathopods. The freshwater members (of Sebidae, Salentinellidae, and Paracrangonyctidae) are hypogean and gnathopods may have become secondarily weakly or not sexually dimorphic. Within the marine leucothoideans, however, members that are morphologically modified in commensal association with tunicates, sponges, and other sessile marine invertebrates (e.g. most Leucothoidae, Vicmusiidae, some Pleustidae, etc), show little or no sexual dimorphism of the gnathopods, except in the microcarnivorous Stenothoidae, and the Anamixidae where modification is extreme (Thomas & Barnard, 1983). Within the Pleustidae, the neopleustinid branch, may have given rise to the Podoceridae (and perhaps the Icilijdae), currently classified within the Corophioidea. These in turn, having strong sexual dimorphism of gnathopods and substrate-clinging life style, have probably given rise directly to the "mainstream" form of the Caprellidea (Laubitz, 1979, 1993). However, the possibility of a polyphyletic origin of the Caprellidea remains investigative (e.g. Laubitz, 1993; Takeuchi, 1993), as is the origin of the Corophioidea (as presently defined). The leucothoid-podocerid-caprellid clade has remained strictly marine, with strong reduction of abdominal and locomotory appendages, and a strong tendency to semi-sessile, commensal, or ectoparasitic life styles.

Conlan (1991) has utilized the earlier version of the phyletic tree to illustrate the taxonomic distribution of mate-guarding and non-mate-guarding behaviour in the Amphipoda. Mate-guarding behaviour had then been formally described within the Gammaroidea, Talitroidea, Hadzioidea, Corophioidea, and Caprellidea, here categorized within the Reptantia. Non mate-guarding behaviour had been observed within the Lysianassoidea, Eusiroidea, Phoxocephaloidea, Pontoporeioidea, and Ampeliscoidea, all categorized here within the Natantia. She also found that species of *Crangonyx* (Crangonyctoidea) and *Haustorius* and *Amphiporeia* (Pontoporeoidea) did not leave the bottom in mate searching, yet also did not mate-carry or mate-guard. Such behaviour, overlapping between Natantia and Reptantia, is not unexpected, and may reveal how similar mating strategies evolved convergently in phyletically unrelated groups exposed to similar environments and edaphic conditions.

Revised Semi-phyletic Classification of the Amphipoda

Phyletically oriented classifications of the Amphipoda proposed by Bousfield (1979a, 1982a, 1983) and embodied in Schram (1986) are revised and updated here (Table III). A closely similar version was published recently by Bousfield and Staude (1994). Although the subordinal and superfamily concepts remain essentially the same, their semi-phyletic arrangement has been altered significantly to conform with the concept of "Natantia-Reptantia" relationships developed in previous sections, and graphically presented in Fig. 30. As we may note below, the families encompassed within several superfamilies have been expanded or modified in the light of recent discoveries and taxonomic advances.

Within the "Natantia" superfamily Lysianassidae is restored to the basic, ancestral position of earlier authors (Sars, 1895; Gurjanova 1951). The list of member families is expanded to include: (1) the Hyperiopsidae and Cyphocaridae, all members of which are neritic, pelagic, and bathypelagic, and the primitive Valettiidae of deep coastal and offshore waters; (2) the fish-parasitic Trischizostomatidae; and (3) the benthic commensal, and modified Conicostomatidae. All of these possess, variously, in combination, the typical lysianassid character states of short swollen peduncular segments and strongly callynophorate flagellum of antenna 1; short rostrum; mouthparts variously modified for carnivory or necrophagy; weakly subchelate, long wristed gnathopod 2 (often with elongate ischium); pleated or convoluted coxal gills; slender or linear brood plates; and (variously) calceolate antennae. Although the Phoxocephaloidea possess more primitive calceoli, and are strongly rostrate, they are ranked phyletically higher because

TABLE III. SEMI-PHYLETIC CLASSIFICATION OF THE AMPHIPOD CRUSTACEANS. (Gammaridea and Ingolfiellidea after Bousfield 1982a, 1983; Hyperiidea after Bowman & Gruner, 1973; Caprellidea after McCain, 1970)

I. AMPHIPODA "NATANTIA"
Superfamily LYSIANASSIDAE (Gammaridea)
1. Valettiidae
2. Hyperiopsidae
3. Cyphocaridae
4. Uristidae
5. Lysianassidae
6. Conicostomatidae
7. Trischizostomatidae
8. Incerta sedis

Superfamily PHOXOCEPHALOIDEA
1. Urothoidae*
2. Platyischnopidae
3. Cheidae
4. Phoxocephalidae
5. Condukiidae

Superfamily SYNOPIOIDEA
1. Synopiidae
2. Argissidae

Superfamily PARDALISCOIDEA
1. Stilipedidae (incl. Astyridae)
2. Pardaliscidae
3. Vitjazianidae

Superfamily STEGOCEPHALOIDEA
1. Stegocephalidae

SUBORDER HYPERIIDEA
INFRAORDER PHYSOSOMATA
Superfamily SCINOIDEA
1. Archaeoscinidae
2. Mimonectidae
3. Proscinidae
4. Scinidae

Superfamily LANCEOLIDEA
1. Microphasmidae
2. Chuneolidae
3. Lanceolidae

INFRAORDER PHYSOCEPHALATA
Superfamily VIBILIOIDEA
1. Vibiliidae
2. Cystosomatidae
3. Paraphronimidae

Superfamily PHRONIMOIDEA
1. Hyperiidae
2. Dairellidae
3. Phronimidae
4. Phrosinidae

Superfamily LYCAEOPSOIDEA
1. Lycaeopsidae

Superfamily PLATYSCELOIDEA
1. Pronoidae; 2. Anapronoidae
3. Lycaeidae; 4. Oxycephalidae
5. Platyscelidae; 6. Parascelidae

Superfamily DEXAMINOIDEA (Gammaridea)
1. Atylidae (+ Lepechinellinae)
2. Dexaminidae (+ Prophliantidae)

Superfamily AMPELISCOIDEA
1. Ampeliscidae

Superfamily PONTOPOREIOIDEA
1. Pontoporeiidae (incl. Bathyporeiidae)
2. Haustoriidae

Superfamily EUSIROIDEA
1. Pontogeneiidae
2. Eusiridae
3. Bateidae
4. Calliopiidae
5. Paraleptamphopidae (incl. Falklandellidae)
6. Gammarellidae
7. Amphithopsidae
8. Gammaracanthidae
9. Paramphithoidae

Superfamily OEDICEROTOIDEA
1. Paracalliopiidae
2. Exoedicerotidae
3. Oedicerotidae

Superfamily MELPHIDIPPOIDEA
1. *Sensonator* group (monotypic)
2. Cheirocratidae (=Hornelliidae)
3. Melphidippidae
4. Megaluropidae
5. Niphargidae? (incert. sed.)
6. Phreatogammaridae? (incert. sed.)

of their loss of callynophore, and their more highly modified mouthparts (lower lip with inner lobes), and unpleated gills. The Synopioidea, Pardaliscoidea and Stegocephaloidea form a non-calceolate core group within Natantia leading to the advanced, parasitoid Hyperiidea, the internal classification of which has been established by Bowman & Gruner (1973).

The weakly or non-rostrate dexaminids and ampeliscids are yet more highly advanced in near loss of callynophore,

TABLE III. (cont'd).

II. **AMPHIPODA "REPTANTIA"**
SUBORDER INGOLFIELLIDEA
1. Ingolfiellidae
2 Metaingolfiellidae

Superfamily CRANGONYCTOIDEA
1. Neoniphargidae (+ Perthiidae)
2. Paramelitidae
3. Sternophysingidae
4. Eocrangonyctidae
5. Crangonyctidae

Superfamily LILJEBORGIOIDEA
1. Liljeborgiidae
2. Paracrangonyctidae
3. Sebidae
4. Colomastigidae
5. Salentinellidae

Superfamily TALITROIDEA
1. Hyalidae (incl. Hyalellidae?)
2. Dogielinotidae
3. Najnidae
4. Ceinidae
5. Eophliantidae
6. Phliantidae
7. Kuriidae
8. Talitridae (4 subgroups)
9. Temnophliantidae

Superfamily LEUCOTHOIDEA
1. Vicmusiidae
2. Pleustidae (12 subf)
3. Acanthonotozomatidae (incl. 3 subf.)
4. Lafystiidae
5. Laphystiopsidae
6. Ochlesidae
7. Amphilochidae (2 subf..)
8. Stenothoidae
9. Cressidae
10. Thaumatelsonidae
11. Maxillipiidae
12. Nihotungidae
13. Pagetinidae
14. Leucothoidae (incl Anamixidae)

Superfamily GAMMAROIDEA)
1. Anisogammaridae
2. Gammaroporeiidae
3. Mesogammaridae
4. Typhlogammaridae
5. Gammaridae
6. Pontogammaridae
7. Acanthogammaridae
8. Macrohectopidae
9. Caspicolidae?
10. Incert. sed.

Superfamily BOGIDIELLOIDEA.
1. Artesiidae
2. Bogidiellidae
3. Kergueleniolidae ?

Superfamily HADZIOIDEA
1. Hadziidae (+ sev. subf.)
2. Metacrangonyctidae
4. Nuuanidae
5. Melitidae
6. Carangoliopsidae
7. Aetiopedidae (transfer from Corophiidae)
8. Allocrangonyctidae (= Pseudoniphargidae)

Superfamily COROPHIOIDEA
1. Ampithoidae*
2. Biancolinidae*
3. Aoridae
4. Cheluridae
5. Isaeidae
6. Ischyroceridae
7. Neomegamphopidae
8. Corophiidae
9. Podoceridae*

SUBORDER CAPRELLIDEA
INFRAORDER CAPRELLIDA
Superfamily PHTISICOIDEA
1. Phtisicidae
2. Dodecadidae

Superfamily CAPRELLOIDEA
1. Caprogammaridae
2. Paracercopidae
3. Caprellidae
4. Aeginellidae

INFRAORDER CYAMIDA
Superfamily CYAMOIDEA
1. Cyamidae

* Possibly convergent within Corophioidea

and weak development of sexually dimorphic gnathopods. The Pontoporeioidea have retained elongate calceolate antennae (male), but lack coxal gill of peraeopod 7, and are allied to the reptant Gammaroidea in possessing sexually dimorphic gnathopods and arostrate head. Freshwater members posses sternal gills. Members of he true Haustoriidae exhibit many character states that are homoplasious with phoxocephaloidean genera (Bousfield, 1989). Despite the lack of calceoli and (with rare exceptions) loss of gnathopod sexual dimorphism, family Haustoriidae continues here to be classified within the Pontoporeioidea on the basis of head form, mouthpart morphology, adactylate peraeopods, strongly deflexed urosome and close similarity of its most primitive members to the sympatric pontoporeiid genus *Amphiporeia*

Within the Eusiroidea may be recognized two main groups: (1) an essentially pelagic, small to medium sized animals that mostly retain brush setae, calceoli, and strongly natatory pleopods and tail fan, and (2) and essentially benthic group of medium to large-sized animals, including the Paramphithoidae, Amphithopsidae, and Gammaracanthidae Bousfield, 1989, have become benthic but lack sexually dimorphic gnathopods and remain essentially marine. Within subgroup (1) the calceolate pontogeneiids and calliopiids have apparently give rise to various groups of Paramoera and allied genera, and to the paraleptamphopid and falklandellid family groups of austral fresh waters. These all tend to have a much reduced uropod 3 and tail fan, but males (in many genera) have developed a pre-amplexing gnathopod 1. Within the closely related but distinctive superfamily Oedicerotoidea, some marine members have retained both calceoli and callynophore, but within estuarine and fresh water exoedicerotids and paracalliopiids (southern hemisphere), males have become larger than females and have convergently (to gammaroideans of the northern hemisphere) developed strongly preamplexing gnathopods and the reproductive "carrying" habit, features convergent with those of gammaroideans of the northern hemisphere. As outlined above, the superfamily Melphidippoidea now encompasses the free-swimming marine Cheirocratidae, the fossorial Megaluropidae, and the primitive para-ancestral freshwater hypogean genus Se*nsonator*. The phyletic status of the freshwater hypogean family Niphargidae, endemic to the European-Mediterranean region, is considered peripherally melphidippoidean, but remains essentially enigmatic.

The order of listing of superfamilies and suborders of Reptantia is essentially that previously arranged in the family tree (p. 126). The primitive Ingolfiellidea are here considered fully subordinally distinct from the Gammaridea (see also p.120).Within the Crangonyctoidea, the rationale of Holsinger (1992a) in separating the Sternophysingidae from the Paramelitidae is recognized here, but family Perthiidae, proposed by Williams and Barnard (1988), is readily encompassed within family Neoniphargidae. The sponge-dwelling Colomastigidae is here formally to transferred from the Leucothoidea to the Liljeborgioidea. Family composition within the Talitroidea remains unchanged, although the freshwater Hyalellidae have proven to be closely allied with *Allorchestes* and other marine genera and may soon be relegated to subfamily status within the Hyalidae.

The concept of superfamily Leucothoidea has been broadened to encompass the Lafystiidae, Acanthonotozomatidae, and Ochlesidae (all transferred from Stegocephaloidea), and the unique pleustid-like Vicmusiidae Just, 1990, recorded from Bass Strait Canyon, Australia. Despite considerable recent taxonomic work on both superfamilies, the family composition of the Gammaroidea and Bogidielloidea remains little changed. The taxonomic refinements within the Hadzioidea have resulted in several new family proposals of which Allocrangonytidae Holsinger, 1989; Nuuanidae McKinney & Barnard, 1977; and Metacrangonyctidae Boutin & Missouli, 1988, are provisionally listed here. The family Aetiopedidae Moore and Myers, 1988, based on an enigmatic new form from the Bass Strait region of Australia, was originally placed within the Corophioidea, but is here transferred to the Hadzioidea. The type species, *Aetiopedes gracilis*, possesses a number of strongly melphidippoidean-hadzioidean and non-corophioidean character states. These include a short antenna 1, posteriorly decreasing size of coxae 1-4, elongate carpus of gnathopods, non-glandular bases and unguiform dactyls of peraeopods 3 & 4, fully biramous and plumose-setose uropod 3, and linear brood plates. The mouthparts appear hadzioidean, and non-corophioidean, especially in the form of maxilla 2 and maxilliped, and in the notched and slightly asymmetrical form of the upper lip.

The concept of superfamily Corophioidea has remained stable following numerous studies by A. A. Myers (loc. cit.) but, under closer numerical taxonomic scrutiny, the concept may prove to be polyphyletic. Thus, ampithoid-biancolinids may form one group, aorid-chelurid-corophiids a second, isaeid-ischyrocerids a third, and the podocerids a fourth, all related more closely to outgroup families within other superfamilies than to each other. Superfamily and family concepts within the Caprellidea accepted here are basically those of McCain (1970) that also take account the high probability of polyphyletic ancestries proposed by Laubitz (1993) and Takeuchi (1993).

In this presentation, we have delved into the pertinency and usefulness of some morphological features for phyletic classification of amphipod crustaceans. A more comprehensive study might have included the classificatory significance of sexual dimorphism of the pleopods, of the form of the rostrum, of segmention of peraeopods, and of several other major characters. We look to eventual establishment of a data base of non-homoplasious character states sufficiently large to employ cladistical analytical methododology with confidence. We urge further study on the significance of surface ultrasture in amphipod pjhylogeny, currently being advanced by Kevin Halcrow (Halcrow & Bousfield, 1987; Halcrow and Powell,1992; Halcrow, 1993). The protein electrophoretic approach that is now providing answers to species level relationships (Bulnheim & Scholl, 1981; Stewart, 1993) might prove applicable at much higher taxonomic levels. Finally, the fundamental work of Sibley and Ahlquist (1983, et sequ.) in which DNA-DNA hybridization techniques were utilized in major phyletic reorganization of avian classification, may eventually be adapted to providing genetic data of exceptional value for the phyletic classification of amphipod crustaceans.

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